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Resource partitioning and browse use by sympatric elk mule deer and white-tailed deer on a winter range in western Montana

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RESOURCE PARTITIONING AND BROWSE USE BY SYMPATRIC ELK, MULE DEER AND WHITE-TAILED DEER ON A WINTER RANGE IN WESTERN MONTANA

By

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ABSTRACT

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Resource Partitioning and Browse Use by Sympatric Elk, Mule Deer and White-Tailed Deer on a Winter Range in Western Montana (228 pp.)

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Wintering ecology and forage relationships of sympatric elk (Cervus elaphus), mule deer (Odocoileus hemionus) and white-tailed deer (O. virginianus), were studied on the Blackfoot-Clearwater Wildlife Management Area from 1991-1994. Twenty vegetation types were delineated along 40 km of transects. Winter aerial counts indicated that cervid densities were about $28/km^2$. Winter mortality, habitat use and distribution of elk, mule deer (MD) and white-tailed deer (WTD) were evaluated by counting carcasses and 61,671 track-sets along 320 km of total transect distance during 1992 and 1993. Cervid spatial distributions were also estimated using radio-telemetry.

Winter carcass densities were $<1/km^2$, and recruitment was slightly greater than regional estimates for elk, MD and WTD. Variability was observed in fecal analysis estimates of cervid diets during both winters. Winter diets of elk were dominated by graminoids, whereas MD and WTD used conifers most. MD and WTD increased use of forbs and low-evergreen shrubs during a mild winter. Tree lichens (Alectoria spp.) were used by elk, MD and WTD. Burned grasslands influenced elk diets more in 1992 than did a harsher winter in 1993. Diets of MD and WTD were most influenced by harsh winter conditions. Variation in habitat selection by cervids was probably in response to forage availability, energetic costs of movement related to snow conditions, and thermal differences between habitats. Elk used large areas comprised of many habitats, and made greatest use of areas with sparse overstory canopy cover. WTD had the smallest herd home range and relied on habitats with abundant overstory canopy. MD used habitats intermediate to those used by elk and WTD. Elk movement appeared least restricted by deep snow. MD used sites with deep-crusted snow (>41 cm) during both winters, but WTD avoided such sites. Resource-use overlap among elk, MD and WTD was relatively low both winters. Overlap was greater between elk and both deer species in 1992, which was influenced by a recent wildfire. Overlap between MD and WTD was low both years because of high spatial separation. High spatial overlap between elk and MD was offset by low dietary similarity. Overall, periods with deep snow did not increase overlap. These results provided evidence that interspecific competition may have functioned in shaping niche relationships. Browse production and utilization varied across types. Sites on south aspects produced more browse and received greater use than sites on north aspects. Serviceberry (Amalanchier alnifolia) was the dominant producer. Browse as sole forage for cervids at observed densities would supply food for about 9 days.

Periodic cervid population reductions in conjunction with prescribed burning would improve productivity of winter forage. More dense-mature conifer stands are needed to provide severe winter cover for WTD. Winter severity indices, browse sampling methods, and vegetation descriptions are also presented.

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In 1987 a young student in wildlife biology approached a bald guy with a funny hat and asked, "how can I make my job application better?" The man's reply was, "This is good . . . but you need more buzzwords!" Since then I have learned many new buzzwords--thanks to Mike Hillis. I am extremely grateful to Mike for his willingness to believe in me from my professional beginning. His encouragement and support are largely responsible for my completion of this project. I owe Mike a great deal for his generous optimism and enduring contributions to my professional experience. Thank you Mike for giving me a chance!

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INTRODUCTION

A resource is a substance or object required by an organism for normal maintenance, growth and reproduction (Ricklefs 1979:878). When resources are in short supply, various forms of interspecific competition can occur (Nelson 1984). Exploitation (Miller 1967) and interference (Denniston 1956) are the most likely forms of competition to play important roles in the interspecific relationships of elk and other large herbivores (Nelson 1982). Interspecific competition may contribute to a decline in the nutritional condition of one or more competing populations, and may ultimately be manifested in reduced population levels or extinctions (Hardin 1960).

Classical studies such as those conducted on warblers (*Dendroica* spp.) (MacArthur 1958) and cormorants (*Phalacrocorax* spp.) (Lack 1945) have demonstrated that similar species can appear to share the same food resources, but minimize competitive interactions through differential selection of space or foods. Other studies have indicated that interspecific competition can potentially limit ungulate populations when habitat overlap occurs. Sinclair (1977:271) suggested that wildebeest (*Connochaetes taurinus*) could significantly limit African buffalo (*Syncerus caffer*) populations when common foraging occurred in riverine grassland habitats. Sinclair (1977:268-269) also noted that intraspecific competition frequently caused density-dependent mortality of adult buffalo during periods of low forage availability.

An abundance of literature on diet similarity among ungulates is partial evidence for considerable interest in interspecific competition (Morris and Schwartz 1957, Hansen and Reid 1975, Hansen and Clark 1977, Hanley and Hanley 1982). However, competition for forage is also influenced by the relative importance of each forage species in shared diets, timing of forage use, duration of forage use, animal distribution, and resource availability (Nelson 1982, 1984). The effects of interspecific competition may be reduced by altering one or several of these factors (Schoener 1974).

Rigorous controlled experiments that provide clear evidence for interspecific competition among large free-ranging species are difficult to accomplish (Connell 1980, Schoener 1983). Consequently, studies of interspecific competition have frequently presented conclusions inferred from results (Schoener 1982). Mackie (1976:49) commented on the subject of interspecific competition among large herbivores stating that "...much of our current thinking remains rooted in inference and speculation, and is controversial at best."

In western Montana, elk, mule deer (MD) and white-tailed deer (WTD) use winter ranges that provide forage, cover and reduced snow accumulations. They occasionally coexist on winter ranges at high densities that might increase interspecific interaction and competition for these resources. This situation was expected on the Blackfoot-Clearwater Wildlife Management Area (BCWMA) because the elk herd had rapidly increased and high MD and WTD densities were observed (M. J. Thompson, Mont. Dep. Fish, Wildl. and Parks, pers. commun.).

Various studies have documented habitat selection and/or forage use by elk, MD or WTD in western Montana (Knoche 1968, Beall 1974, Marcum 1975, Scott 1978, Berner 1985, Seeley 1985, Hicks 1990, Stansberry 1991 and Hurley 1994). Other studies have investigated relationships among sympatric ungulates (Smith and Julander 1953, Mackie 1970, Bell 1971, Constan 1972, Kramer 1973, Hirst 1975, Hudson et al. 1976, Telfer 1978, Singer 1979, Salter and Hudson 1980, Schwartz and Ellis 1981, Hanley and Hanley 1982, Wydeven and Dahlgren 1985, Jenkins and Wright 1988), but little is known about the winter ecology of sympatric elk, MD and WTD in a situation similar to that on the BCWMA.

Jenkins and Wright (1988) studied spatial, habitat and dietary overlap among wintering moose (Alces alces), elk and WTD in the North Fork of the Flathead River Basin in northwestern Montana. They found competition for browse between elk and WTD was greatest during severe winters when grasses preferred by elk were unavailable. Although Jenkins and Wright (1988) found little evidence of competition between WTD and elk overall, higher elk and deer densities and lower inherent vegetative productivity on the BCWMA were expected to increase the potential for competition (Julander 1958, Mackie 1970, Greer et al. 1970). Further, Jenkins and Wright (1988) did not evaluate the effects of cumulative browsing by elk and deer on the browse forage-base, or the capacity of the browse to sustain 3 cervid populations winter after winter. Finally, they compared resource-use overlap between winters, but did not consider potential variability in competition within a single winter.

This study, conducted from 1991-1994 was an extension of earlier research on the BCWMA (1984-1989), which documented ecology and harvest relationships of elk (Hurley 1994). Hurley (Univ. Idaho, Moscow, pers. commun.), hypothesized that browse availability and cervid competition were potential limiting factors to elk and deer populations on the BCWMA.

While the BCWMA elk population was well known, comparatively little was known about the sympatric deer populations. Janke (1977) and Slott (1980) described WTD winter ranges, populations, and habitats along the lower Clearwater River. However, little information was available on the degree of browse utilization and habitat use by WTD on the BCWMA winter range where considerable spatial overlap with elk was expected. Little information of any sort was available on the MD population.

OBJECTIVES

The purpose of this research was to evaluate spatial, habitat and dietary overlap among elk, MD and WTD on the BCWMA; and to estimate browse productivity and use by cervids. This broad objective was divided into more specific objectives that form four chapters of this thesis:

1. Delineate and describe plant communities on the BCWMA.
2. Evaluate the use of space, habitats and forage by the three cervid populations, and estimate the degree of resource-use overlap between cervid populations.
3. Document browse production, utilization and condition, and the effects of utilization on 6 palatable shrub species found on the BCWMA.
4. Use the combined information to assess the potential for interspecific competition and the effects of that competition on the welfare of each cervid population.

STUDY AREA

General Description

The study area was located about 70 km northeast of Missoula, Montana (Fig. 1). The core winter range covered about 9,000 ha within Montana Department of Fish, Wildlife and Parks (MDFWP) hunting district 282. Elevations ranged from 1,189-1,707 m and topography was predominantly gentle. Steeper slopes from 21-60% were commonly associated with

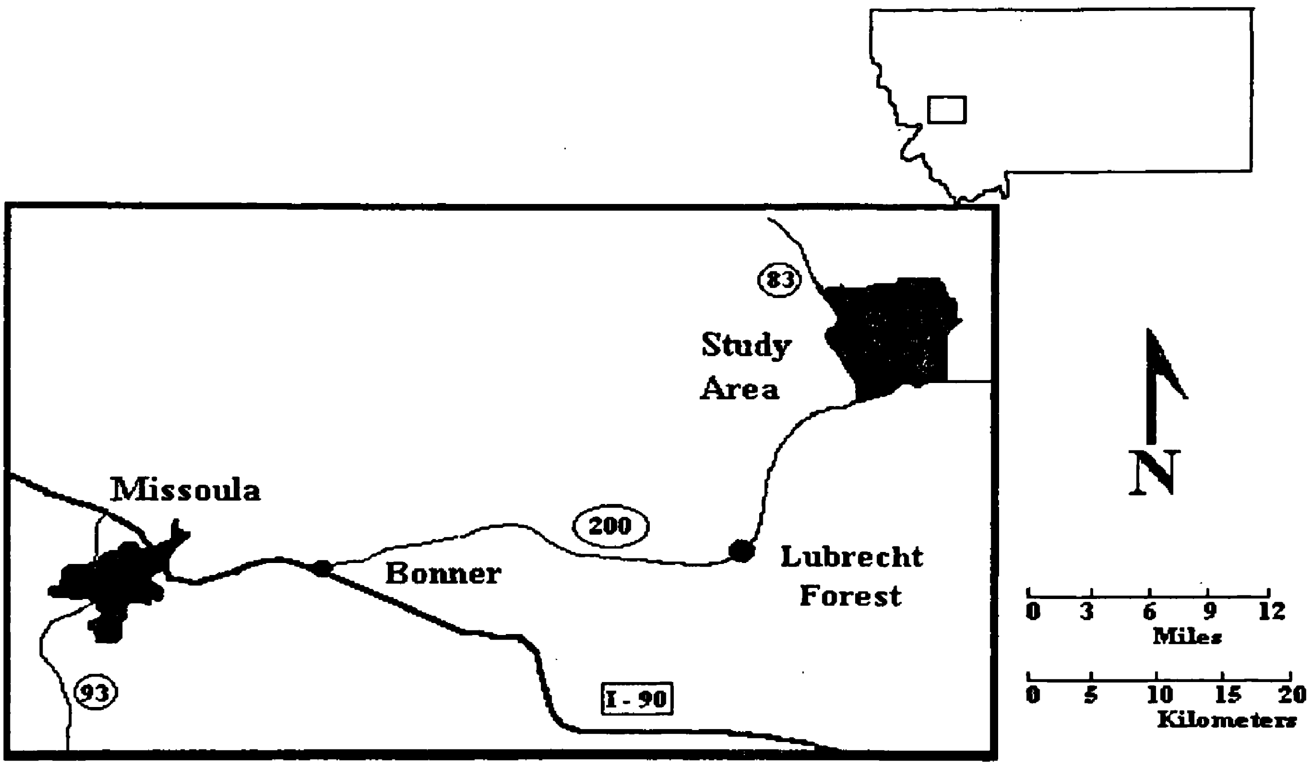


Figure 1. Study area location in western Montana.

forested habitats on Boyd and Sperry Mountains. The Clearwater and Blackfoot Rivers bordered the study area along the west and south respectively. The north and east sides were bounded by the Woodworth Road.

Land ownership of hunting district 282 was approximately 45% Plum Creek Timber Corporation, 20% MDFWP, 20% Department of State Lands, 8% private, 4% Montana Forest and Conservation Experiment Station, and 3% U.S. Bureau of Land Management. Livestock grazing had been excluded from the primary wintering area since 1948 to reserve winter forage for elk and deer.

Hunting district 282 was primary winter range for elk and deer herds whose summer ranges encompassed about 1,400 km^2. The majority of the summer range was managed by the Lolo National Forest. Each of the aforementioned land owners had unique land management objectives, which influenced habitat for cervids.

Prior to the 1970's, the BCWMA was managed by MDFWP to mitigate potential forage depredation by elk on adjacent private land. From the 1980's to the present, management objectives have stressed maximizing the number of migratory elk that the winter range could support (BCWMA Draft Rev. Manage. Plan, MDFWP, Missoula, 1989). These objectives were to be met while maintaining or enhancing the condition of wintering elk and deer populations.

Climate

Characteristic weather patterns generally originate from the Pacific Ocean, and air masses move from west to east. Mean monthly temperatures normally range from about -8.4° C in January to 16.8° C in July (Steele 1981). Annual precipitation ranges from 30-75 cm with a mean of about 45 cm (Steele 1981). Summers are hot and dry and over 66% of the annual precipitation frequently falls from December through June (Steele 1978). Winter snow accumulations on nearby summer ranges, at elevations >1,800 m, commonly exceed depths of 100 cm.

Weather was variable during the winters of 1992 and 1993. Although little difference was observed in total monthly precipitation between years, there was a marked difference in average daily temperatures (Fig. 2) and snow accumulations (Fig. 3).

Vegetation

General vegetation cover types for hunting district 282 were 63% forested (50% open-canopy, 8% moderately open-canopy, 5% closed-canopy timber) 28% rangeland, 3% hay fields, 3% aspen/shrubs and 3% moist meadows (DelSordo 1993). For this study the forested and rangeland types were of primary interest.

The forest overstory was dominated by second growth Douglas-fir (<u>Pseudotsuga menziesii</u>) stands >12 m tall with

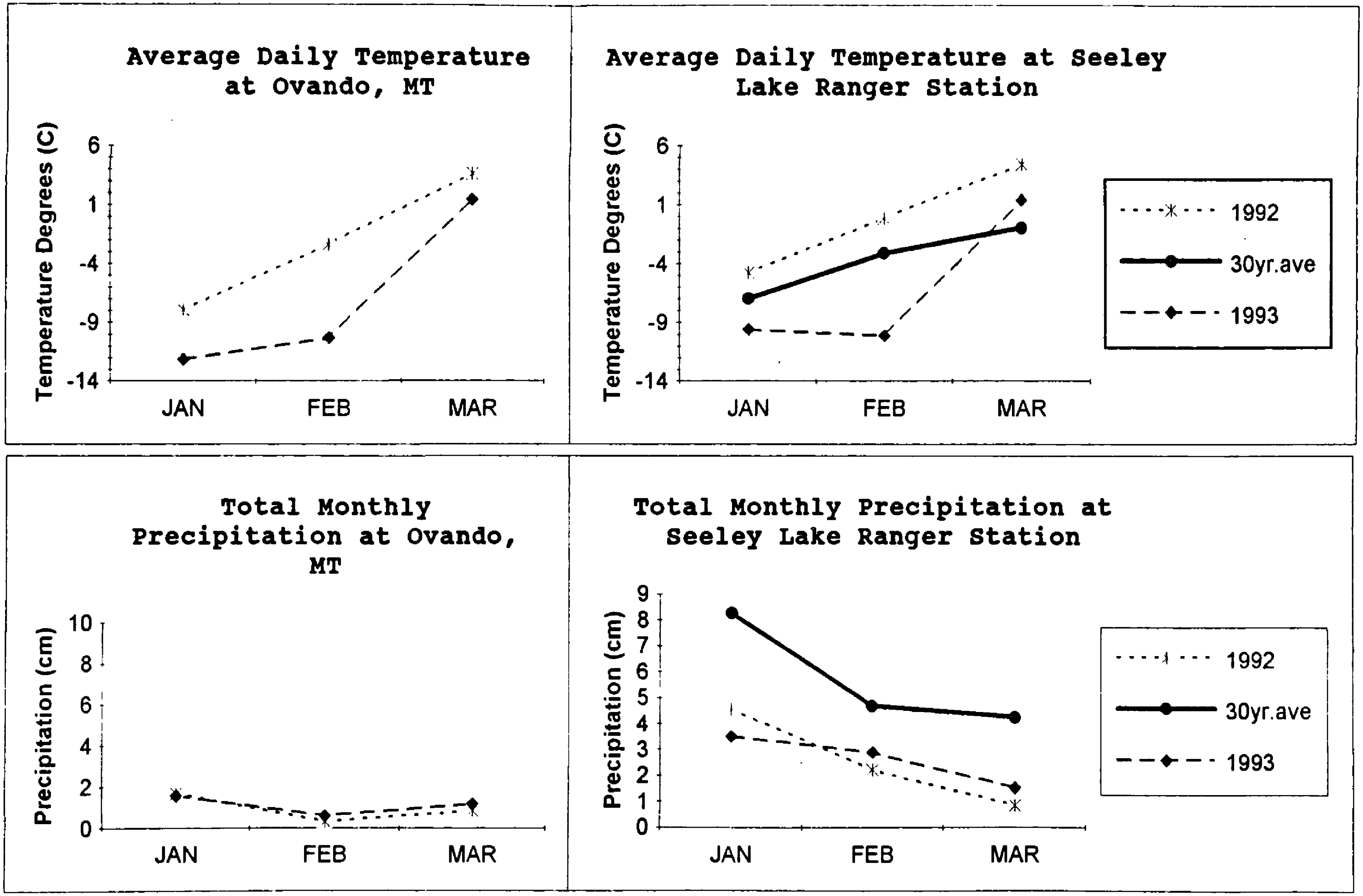


Figure 2. Average daily temperatures and total monthly precipitation at Ovando and Seeley Lake, Montana for 3 winter months during 1992 and 1993 (Local Climatological Data, National Weather Service, Missoula, Montana).

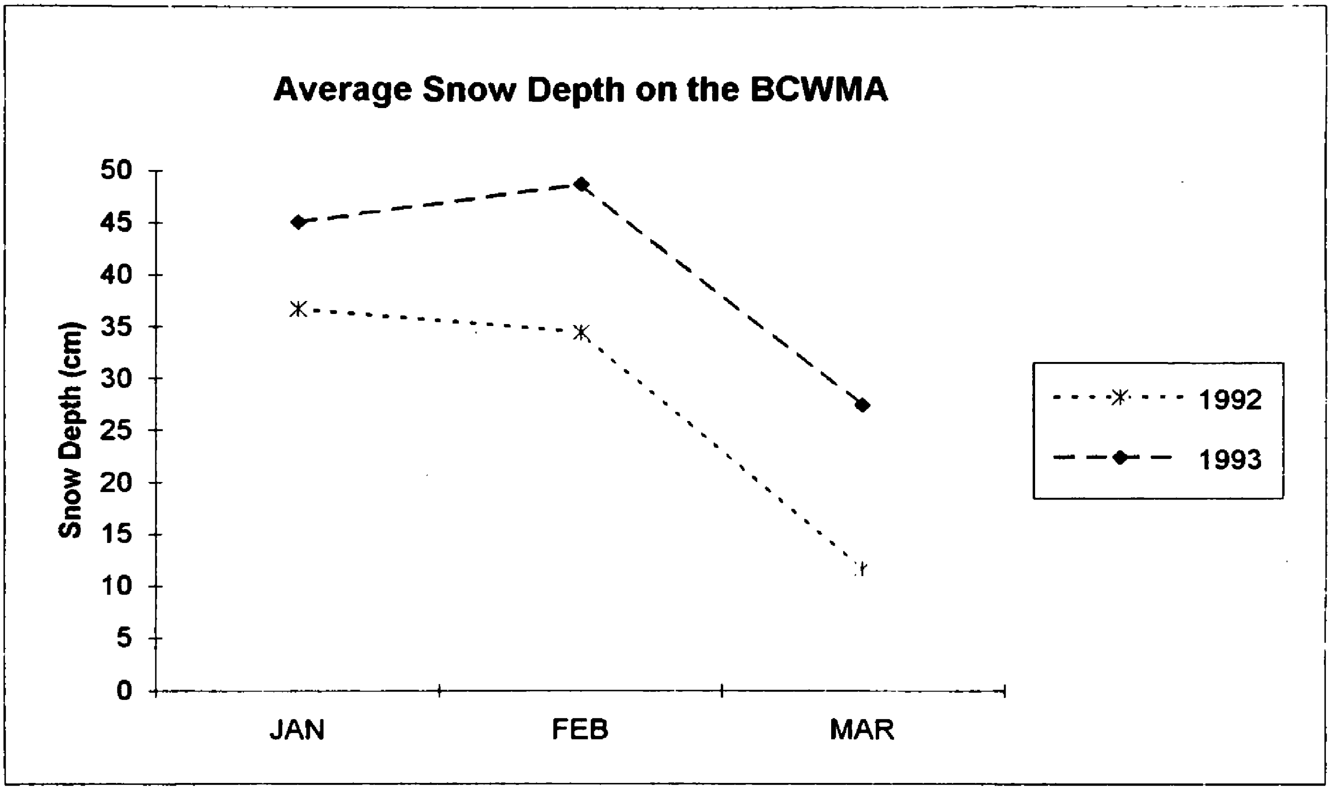


Figure 3. Monthly average snow depths on the BCWMA during the winters of 1992 and 1993.

sparse canopies and well developed shrub and patchy Douglas-fir sapling understories. These stands remained after extensive logging over the past 60 years. Mature ponderosa pine (*Pinus ponderosa*) stands were common along the western border of the study area and along forest-bunchgrass ecotones. Mixed stands of western larch (*Larix occidentalis*), sub-alpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea englemannii*), lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) were typical of cool or moist sites.

Forest understory vegetation was relatively homogeneous and contained snowberry (*Symphoricarpos albus*), serviceberry (*Amelanchier alnifolia*), Oregon grape (*Berberis repens*), spiraea (*Spiraea betulifolia*), elk sedge (*Carex geyeri*), pine grass (*Calamagrostis rubescens*), common yarrow (*Achillea millefolium*) and wild strawberry (*Fragaria virginiana*). Palatable shrub species displayed evidence of past heavy browsing by cervids, and were perpetuated by infrequent wildfires and logging disturbance.

Common plant species found in grasslands included rough fescue (*Festuca scabrella*), bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*F. idahoensis*), prairie junegrass (*Koeleria cristata*), bluegrass (*Poa* spp.), threadleaf sedge (*C. filifolia*), spotted knapweed (*Centaurea maculosa*), arrowleaf balsamroot (*Balsamorhiza sagittata*), lupine (*Lupinus* spp.) and sticky geranium (*Geranium viscosissimum*).

For reference, common and scientific names of all understory plant species listed hereafter are included in Appendix A. Plant nomenclature followed Hitchcock and Cronquist (1973).

Cervid Population Estimates

About 100-200 elk wintered on the BCWMA at the time of its purchase in 1948. Elk numbers gradually increased and ranged from 400-800 during the 1960's and 1970's (M. J. Thompson, MDFWP, pers. commun.). By 1980 MDFWP had initiated a regulated cow harvest permit system in surrounding hunting districts, which along with several mild winters, resulted in additional population increases. An aerial count conducted by MDFWP on 10 December 1986 revealed 1,085 elk (MDFWP, unpubl. data). From 1985-1989 the wintering elk population was generally believed to be about 1,200. More refined aerial estimates (following Samuel et al. 1987) made from 1988 to 1993 indicated that elk numbers were gradually decreasing.

Past MD population levels were virtually unknown. MD were frequently observed during BCWMA wildlife surveys conducted in the 1940's and 1950's (MDFWP, survey notes, unpubl. data), and 367 MD were counted during the 10 December 1986 elk survey (MDFWP, unpubl. data).

Observers in 1954 postulated that high densities of WTD along the Clearwater River and western portion of the BCWMA could not be sustained. Several of these observers also described browse resources in the area as seriously over-used (MDFWP, survey notes, unpubl. data). Hartkorn and Rognrud (1956) estimated winter WTD densities along the Clearwater River at 50 deer/km^2. This 1956 density estimate coincided with the highest winter mortality estimated (35 dead deer/km^2) on the area during the past 30 years (MDFWP, lower Clearwater River dead deer surveys, unpubl. data). Janke (1977) and Slott (1980) later estimated WTD populations along the lower Clearwater River at 21-29 deer/km^2, which placed herd estimates at about 400-550 from 1976 to 1979. Harvest data for the vicinity have suggested a steady increase in WTD numbers since 1979 (M. J. Thompson, MDFWP, pers. commun.).

October 1991 Wildfire

On 12 October 1991, a wildfire burned approximately 25% of hunting district 282 in less than 24 hours. The burn was confined to the southern portion of the study area. Of the area that burned approximately 35% was rough fescue grassland and 65% was forested or partially forested. Although various burn intensities were observed, burn effects in forested areas were generally severe due to dry windy conditions at the time of the fire. The timing, intensity and magnitude of the burn further increased the potential for interspecific competition among elk and deer during the winters of 1992 and 1993.

CHAPTER I: PLANT COMMUNITIES

INTRODUCTION

A detailed vegetation classification was essential to document habitat use by cervids on the BCWMA. DelSordo (1993) described and mapped vegetation types on the study area. However, DelSordo's classification did not consider species and structural changes brought about by the 1991 wildfire. Further, more site specific data were needed to adequately evaluate resource-use overlap by cervids.

Overstory structure, understory structure and topographic variables were emphasized in this classification because they were expected to influence cervid use of space, habitats and forage during winter (Jenkins 1985). Tree species composition was considered in the classification as a relative indicator of site potential and productivity.

METHODS

Transect Layout

I established five transects running from a northwest to southeast direction (160° azimuth) (Fig. 4). This orientation was selected to minimize contouring across steep slopes during winter track counts. The position of transect

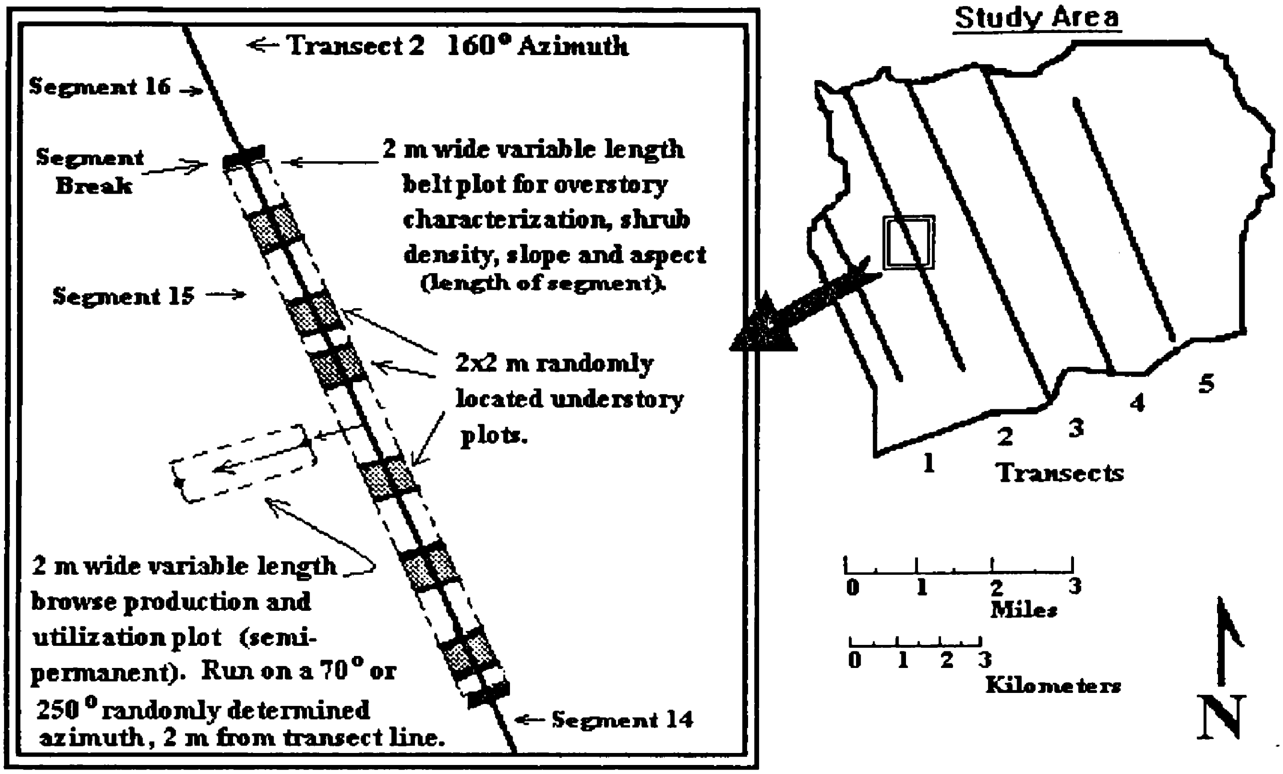


Figure 4. Transect and vegetation plot layout on the BCWMA.

1 was selected by establishing a point on a USGS 1:24,000 topographic map approximately 400 m east of Highway 83. Transects 2-5 were then positioned at 1-mile intervals east of transect 1 (Fig. 4). Each transect was about 8 km long and was assumed to intersect vegetation communities in proportion to their availability.

I divided each transect into semi-permanently marked segments (191 total). Segment breaks were based upon obvious changes in overstory and understory species composition and structure, slope and aspect. Segment lengths were determined by pacing, and were adjusted using correction factors determined for 30 measured segments with steep (≥40%) and gentle (<40%) slopes. Segment endpoints were marked with colored vinyl flagging and green timber marking paint. Additional trees were marked as needed along transects to facilitate course repeatability during sampling. Segments in homogeneous stands that exceeded 400 m were divided to reduce variation in track densities caused by excessive segment lengths. Habitat segments <65 m long were combined with the most similar adjacent segment.

Sampling Methods

I estimated slope and aspect at 5 evenly spaced points, from a random origin, along each segment using a clinometer and compass. Three to 5 azimuth readings (falling in the same 180° compass region) were averaged to generate the prevailing segment aspect. The elevation for each segment midpoint was estimated using USGS 1:24,000 topographic maps.

Overstory stand structure and tree species composition for each segment were estimated by counting all trees by size class and species that occurred within 2 m wide belt plots centered on each transect (Fig. 4). Belt plots ran the length of each segment. Tree density estimates were derived for each belt plot and were converted to stems/ha. Basal area (m^2/ha) for each belt plot was calculated from estimates of tree density by diameter class and 7 diameter class midpoints (M. Sweet, Univ. Mont., pers. commun.). Overstory canopy cover >6.1 m high was estimated for each segment at 10 evenly spaced locations (with random origin) using a gridded convex mirror. Deciduous leaf cover was excluded from canopy cover estimates because it did not contribute to canopy closure in winter.

Understory species composition and frequency for segments >100-m-long were quantified by establishing 10, 4 m^2 (2m x 2m) stratified-random understory plots (Fig. 4). The understory sampling intensity for segments <100 m long was 1 understory plot for every 10 m of belt plot length (e.g. an 87 m belt plot contained 8 understory plots). A square frame, sized to encompass 5% of the plot area, was placed in each plot as a template to standardize ground cover estimates. Ground cover was estimated to the nearest

1.0% for all forbs, graminoids and shrubs. Percentage cover totaled 100% for each plot.

I estimated relative shrub densities along each belt plot by counting single stems, or clumped stem aggregations of the same species (defined as "canopies") that were spatially separated by at least 0.5 m. Therefore, a "canopy" was composed of one or many individual stems (Fig. 5). Shrub canopies were tallied in 1 of 7 height classes by species. Shrub height was defined as the average height of the 2 tallest mainstems within a canopy. Shrub canopy densities/m^2 were subsequently converted to density/ha for each belt plot. Shrub biomass indices for habitat classifications were calculated by multiplying shrub canopy density by the shrub height mean for a belt plot. These techniques were feasible on the BCWMA because shrub crown size relative to shrub height was fairly constant, and shrubs growing in continuous mats were never observed. Shrub biomass weights were not estimated.

Data Analysis

I entered all vegetation data into the Foxpro 2.0 database management system in DBF file format and converted the files to Microsoft Excel 3.0 XLS spreadsheet files for manipulation. Means for topographic, overstory and understory variables were calculated by segment. I selected 14 variables for vegetation type characterization: conifer

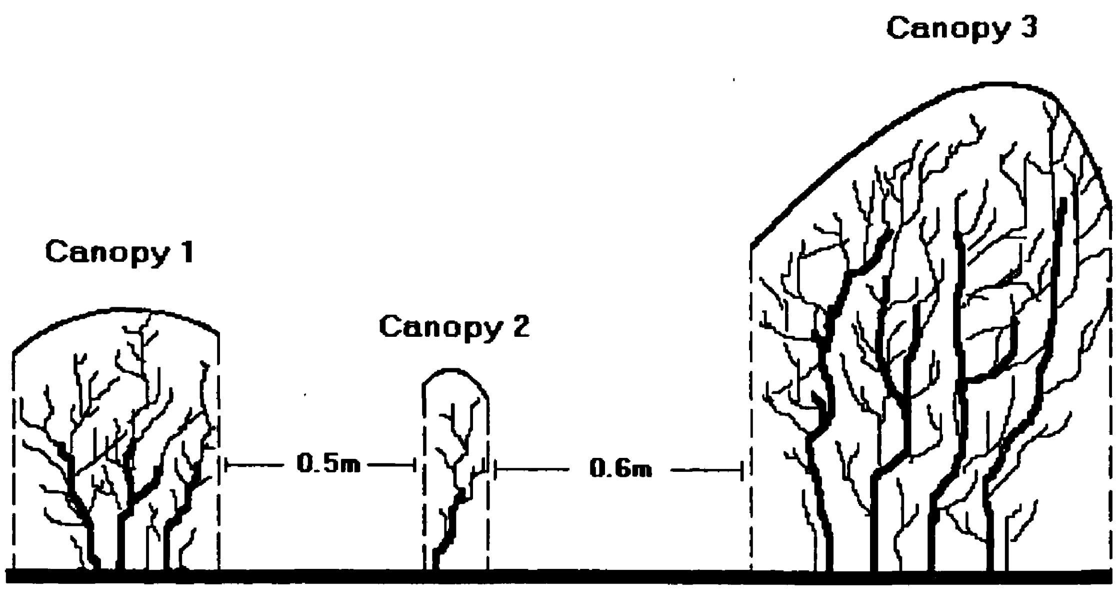


Figure 5. Diagram displaying the arrangement of 3 distinct shrub canopies made up of 3, 1, and 4 mainstems respectively.

seedling density, tree stem density >38 cm dbh, total tree stem density, basal area, mean tree dbh, % overstory canopy cover, % Douglas-fir composition, % ponderosa pine composition, % aspen composition, shrub canopy density, shrub height, shrub biomass index, slope, and aspect. Z-values for the 14 variable means for each segment were used to combine similar segments into broader habitat categories using the SPSSx command "Cluster" for 40 clusters and "Average Linkage"- Between Groups (Norusis 1988). Remaining single segments were combined with similar clusters or were omitted (n=2). Burned segments were placed in broad habitat categories based on burn severity, live tree densities, dead tree densities, basal area and overstory canopy cover. Characteristic understory species for the derived habitat categories were defined as the 4 most abundant and 4 most frequent species encountered. Understory ground cover results were used for descriptive purposes, but were not used to derive habitat classifications.

RESULTS

Fifteen vegetation types characterized the unburned portion of the study area and 5 characterized the burned portion (Table 1). Structural characteristics of the overstories and understories of these 20 types are summarized in Tables 2 and 3. Variables characterizing burn intensity and severity for the 5 burned types are summarized

Table 1. Characteristics of unburned and burned vegetation types determined from 191 stands on the BCWMA.

Unburned Types and (% survey distance)	Description*	Characteristic Understory Species
Rough Fescue/ Grassland (3.5)	Overstory absent (0% cover),shrub layer absent (<12 can/ha), and well developed herbaceous layer.	*Agropyron spicatum, Carex filifolia, Festuca idahoensis, F. scabrella, Koeleria cristata, Balsamorhiza sagittata, Centaurea maculosa, Lupinus spp.*
Douglas-fir/ Seed Tree (3.5)	Poorly developed overstory (5% cover), species composition (63% DF, 27% WL, 10% other), sparse shrub layer (917 can/ha), and well developed herbaceous layer.	*Berberis repens, Spiraea betulifolia, Symphoricarpos albus, C. geyeri, Calamagrostis rubescens, Centaurea maculosa, Epilobium angustifolium, Fragaria virginiana.*
Aspen (2.0)	Open overstory (20%cover), species composition (58% aspen, 35% DF, 7% PP), well developed shrub layer (1,927 can/ha), and well developed herbaceous layer.	*Amelanchier alnifolia, B. repens, Rosa woodsii, S. betulifolia, S. albus, C. geyeri, C. rubescens, F. virginiana.*
Ponderosa Pine (5.5)	Open overstory (22% cover), species composition (79% PP, 21% DF), poorly developed shrub layer (312 can/ha), and well developed herbaceous layer.	*A. spicatum, F. scabrella, Poa spp., Achillea millefolium, C. maculosa, Geranium viscosissimum, Lupinus spp., Potentilla spp.*
Subalpine fir/ Overstory Removal (2.0)	Open overstory (24% cover), species composition (40% SF, 35% DF, 13% spruce, 8% WL, 4% other), poorly developed shrub layer (431 can/ha), and a well developed herbaceous layer.	*Menziesia ferruginea, Pachistima myrsinites, S. betulifolia, Vaccinium globulare, C. rubescens, Arnica spp., Linnaea borealis, Xerophyllum tenax.*
Douglas-fir/ Open (9.9)	Open overstory (27% cover), species composition (88% DF, 3% PP, 9% other), well developed shrub layer (1,834 can/ha), and well developed herbaceous layer.	*A. alnifolia, B. repens, S. betulifolia, S. albus, C. geyeri, A. millefolium, Aster conspicuus, F. virginiana.*
Douglas-fir/ (Xeric) (10.4)	Open overstory (29% cover), species composition (92% DF, 5% PP, 3% other), sparse to well developed shrub layer (1,498 can/ha), and well developed herbaceous layer.	*A. alnifolia, B. repens, S. betulifolia, S. albus, C. geyeri, C. rubescens, A. conspicuus, F. virginiana.*
Douglas-fir/ Open (Cool) (10.9)	Moderately open overstory (32% cover), species composition (80% DF, 11% WL, 6% spruce, 3% other), well developed shrub layer (2,034 can/ha), and well developed herbaceous layer.	*Acer glabrum, A. alnifolia, B. repens, S. betulifolia, S. albus, C. geyeri, C. rubescens, F. virginiana.*
Spruce (1.5)	Well developed overstory (41% cover), species composition (30% spruce, 26% DF, 17% WL, 15% blk. cottonwood, 11% aspen), dense shrubs (3,142 can/ha) and well developed herbaceous layer.	*A. alnifolia, B. repens, Cornus stolonifera, S. betulifolia, S. albus, C. rubescens, Arnica spp., F. virginiana.*
Douglas-fir/ (Cold) (2.5)	Well developed overstory (44% cover), species composition (82% DF, 12% WL, 4% LPP, 2% other), sparse shrub layer (1,157 can/ha), and well developed herbaceous layer.	*A. alnifolia, B. repens, S. betulifolia, S. albus, C. geyeri, C. rubescens, F. virginiana, Thalictrum occidentale.*
Subalpine fir (1.0)	Well developed overstory (48% cover), species composition (46% SF, 24% DF, 16% WL, 12% spruce, 2% other), sparse shrub layer (780 can/ha), and well developed herbaceous layer.	*M. ferruginea, S. betulifolia, V. globulare, C. geyeri, C. rubescens, Arnica spp., L. borealis, T. occidentale.*
Douglas-fir,Larch/ Poles (6.0)	Well developed overstory (50% cover), species composition (52% DF, 38% WL, 10% other), sparse shrub layer (1,237 can/ha), moderately developed herbaceous layer and abundant litter.	*A. alnifolia, B. repens, S. betulifolia, C. geyeri, C. rubescens, Arnica spp., F. virginiana, T. occidentale.*
Mixed Conifer (1.0)	Well developed overstory (52% cover), species composition (27% DF, 23% spruce, 18% SF, 14% LPP, 18% other), sparse shrub layer (954 can/ha), moderately developed herbaceous layer.	*Arctostaphylos uva-ursi, B. repens, S. betulifolia, S. albus, C. rubescens, Arnica spp., F. virginiana, L. borealis.*
Douglas-fir/ Mature (3.5)	Well developed overstory (53% cover), species composition (84% DF, 16% PP), well developed shrub layer (2,156 can/ha), moderately developed herbaceous layer and abundant litter.	*A. alnifolia, S. betulifolia, S. albus, C. geyeri, C. rubescens, A. millefolium, B. sagittata, Penstemon spp.*
Ponderosa Pine/ Mature (3.0)	Well developed overstory (53% cover), species composition (94% PP, 5% DF, 1% aspen), sparse shrub layer (1,147 can/ha), moderately developed herbaceous layer and abundant litter.	*S. albus, A. spicatum, C. geyeri, F. scabrella, Poa spp., A. millefolium, B. sagittata, Potentilla spp.*

Table 1. Continued.

Burned Types and (% survey distance)	Description*	Characteristic Understory Plant Species
Grassland (11.9)	Poorly developed overstory (2% cover), species composition (90% PP, 10% aspen), shrubs absent (3 can/ha), and moderately well developed herbaceous layer.	*A. spicatum, C. filifolia, F. idahoensis, F. scabrella, K. cristata, Poa spp., A. millefolium, Lupinus spp.*
Cutover Conifer/ Intense Burn (9.9)	Poorly developed overstory (2% cover), species composition (70% DF, 14% PP, 11% WL, 5% other), sparse shrub layer <1 m high (688 can/ha), and poorly developed herbaceous layer.	*B. repens, S. betulifolia, S. albus, C. geyeri, C. rubescens, A. conspicuus, C. maculosa, Lupinus spp.*
Young Conifer/ Intense Burn (2.0)	Poorly developed overstory (3% cover), species composition (40% PP, 37% DF, 13% WL, 10% aspen), poorly developed shrub layer (327 can/ha), and sparse herbaceous layer.	*B. repens, S. betulifolia, S. albus, C. rubescens, Arnica spp., A. conspicuus, E. angustifolium, Lupinus spp.*
Conifer/ Moderate Burn (4.0)	Sparse overstory (17% cover), species composition (53% DF, 24% PP, 12% WL, 11% aspen), well developed shrub layer <1 m high (2,070can/ha), and sparse herbaceous layer.	*A. alnifolia, S. betulifolia, S. albus, C. geyeri, C. rubescens, Arnica spp., Brassicaceae family, Lupinus spp.*
Conifer/ Light Burn (6.0)	Sparse overstory (18% cover), species composition (46% DF, 33% PP, 20%aspen, 1% other), sparse to well developed shrub layer <1 m high (1,495 can/ha), and moderately well developed herbaceous layer.	*S. albus, F. scabrella, Scirpus microcarpus, A. millefolium, B. sagittata, C. maculosa, Cirsium spp., Lupinus spp.*

* Values of overstory cover, species composition and shrub density in canopies/ha (can/ha) are mean measurements of 2-23 stands. Tree species abbreviations are DF=Douglas-fir, LPP=lodgepole pine, PP=ponderosa pine, SF=subalpine fir, WL=western larch.

Table 2. Mean overstory and topographic characteristics (and SE) of vegetation types determined from 191 stands on the BCWMA.

Community Type Unburned	n	Overstory Cover %	Tree Density (Stems/ha)	Tree Basal Area (sq. m/ha)	Tree DBH (cm)	Density of Trees >38 cm DBH (Stems/ha)	Slope %	Dominant Aspect	Elevation (m)
Rough Fescue/ Grassland	4	0(0.0)	18(7.9)	0.5(0.2)	14(4.8)	0(0.0)	19(3.3)	S	1,353(28.6)
Douglas-fir/ Seed Tree	5	5(1.1)	452(36.9)	5(1.5)	10(1.1)	0(0.0)	17(2.3)	N	1,512(55.8)
Aspen	5	20(4.3)	1,575(240.6)	17(4.0)	14(1.2)	15(9.6)	9(1.6)	SW	1,422(35.3)
Ponderosa Pine	11	22(4.0)	318(106.1)	10(1.4)	23(4.0)	23(6.6)	17(1.2)	SW	1,302(18.9)
Sub-alpine fir/ Overstory removal	4	24(3.1)	1,251(264.7)	17(2.0)	11(1.0)	0(0.0)	33(1.8)	N	1,537(17.3)
Douglas-fir/ Open	19	27(2.3)	620(90.5)	16(1.3)	17(1.0)	18(6.2)	12(1.0)	SE	1,408(17.0)
Douglas-fir (Xeric)	21	29(3.0)	547(63.7)	13(1.1)	17(1.4)	16(3.9)	34(1.9)	S	1,492(21.1)
Douglas-fir/ Open (Cool)	23	32(1.7)	736(74.0)	17(1.3)	15(0.7)	17(5.5)	15(1.3)	N	1,356(8.4)
Spruce	4	41(5.5)	1,301(189.0)	30(4.5)	17(1.8)	42(25.0)	10(4.0)	N	1,348(6.3)
Douglas-fir (Cold)	8	44(3.5)	996(126.3)	20(2.2)	14(0.6)	12(8.9)	23(4.1)	N	1,353(20.5)
Sub-alpine fir	2	48(9.5)	1,080(17.5)	35(1.0)	15(0.4)	88(5.7)	14(4.5)	N	1,570(15.2)
Douglas-fir/Larch Poles	11	50(3.7)	1,152(194.3)	25(1.8)	17(1.1)	16(6.1)	45(4.3)	N	1,442(34.1)
Mixed Conifer	3	52(12.0)	1,634(592.1)	27(3.9)	15(2.3)	13(12.6)	11(1.5)	N	1,346(2.7)
Douglas-fir/ Mature	7	53(4.5)	513(193.4)	38(3.4)	34(5.8)	108(7.9)	47(6.0)	SW	1,409(49.6)
Ponderosa Pine/ Mature	6	53(3.5)	299(100.9)	25(1.7)	34(4.4)	73(9.6)	16(5.1)	SW	1,272(15.5)

Table 2. Continued.

Community Type Burned	n	Overstory Cover %	Total Tree Density (Stems/ha)*	Live Trees >38 cm DBH (Stems/ha)	Live Tree DBH (cm)*	Live Conifers %	Charred Snags <25cm DBH (Stems/ha)*	Charred Snags 25-51 cm DBH (Stems/ha)	Slope %	Dominant Aspect	Elevation (m)
Grassland	15	2(0.8)	124(88.1)	3(2.7)	10(4.4)	61(10.7)	9(5.1)	1(1.4)	8(1.0)	SW	1,236(21.0)
Cutover Conifer/ Intense Burn	20	2(0.3)	320(61.9)	0(0.0)	3(1.8)	2(1.4)	277(59.7)	33(7.9)	32(2.6)	N	1,380(13.7)
Young Conifer/ Intense Burn	4	3(1.4)	790(216.7)	4(3.6)	2(1.7)	1(1.1)	646(144.8)	11(11.0)	29(7.6)	N	1,323(14.5)
Conifer/ Moderate Burn	7	17(4.8)	726(186.8)	29(15.0)	24(6.4)	40(12.8)	274(67.7)	53(16.0)	43(7.7)	N	1,342(22.4)
Conifer/ Light Burn	12	18(3.2)	2,230(1417.1)	20(10.6)	15(3.5)	66(9.7)	74(32.6)	8(6.1)	29(6.8)	S	1,283(19.5)

* Estimates include tree seedling size class.

Table 3. Mean understory and burn characteristics (and SE) of vegetation types determined from 191 stands on the BCWMA.

Community Type Unburned	n	Conifer Seedling Density (Stems/ha)	Shrub Canopy Density (canopies/ha)	Shrub Height (m)	Shrub Density X Height/100 (Biomass Index)
Rough Fescue/ Grassland	4	30(17.3)	12(8.8)	1.2(1.1)	0.6(0.6)
Douglas-fir/ Seed Tree	5	2,263(550.6)	917(291.0)	0.8(0.1)	9.7(2.6)
Aspen	5	326(102.9)	1,927(425.7)	1.3(0.2)	33.6(9.6)
Ponderosa Pine	11	751(274.4)	312(103.5)	0.5(0.1)	1.9(0.8)
Sub-alpine fir/ Overstory removal	4	4,766(544.2)	431(9.0)	1.2(0.3)	6.8(1.5)
Douglas-fir/ Open	19	694(81.3)	1,834(171.8)	1.2(0.1)	29.0(3.8)
Douglas-fir (Xeric)	21	528(122.6)	1,499(180.7)	0.6(0.0)	12.5(1.9)
Douglas-fir/ Open (Cool)	23	991(132.1)	2,034(120.8)	1.3(0.1)	34.4(2.7)
Spruce	4	1,011(311.1)	3,142(451.7)	1.4(0.1)	58.5(11.2)
Douglas-fir (Cold)	8	1,188(313.1)	1,157(238.8)	0.6(0.1)	9.9(2.4)
Sub-alpine fir	2	4,870(1106.2)	780(65.3)	2.1(0.1)	21.7(0.8)
Douglas-fir/Larch Poles	11	927(297.9)	1,237(342.7)	0.7(0.1)	13.0(3.8)
Mixed Conifer	3	721(325.4)	954(147.3)	0.6(0.1)	7.7(1.9)
Douglas-fir/ Mature	7	367(195.6)	2,156(478.5)	0.4(0.1)	13.3(4.3)
Ponderosa Pine/ Mature	6	349(258.6)	1,147(750.0)	0.5(0.2)	7.3(4.8)

Table 3. Continued.

Community Type Burned	n	Live Conifer Seedling Density (Stems/ha)	Shrub Canopy Density (canopies/ha)	Shrub Height (m)	Shrub Density X Height/100 (Biomass Index)	Scorch Height (m)	Distance Burned %
Grassland	15	0(0.0)	3(2.0)	0.03(0.02)	0(0.0)	0.9(0.1)	91(5.5)
Cutover Conifer/ Intense Burn	20	1(1.1)	688(141.4)	0.37(0.05)	4.2(0.9)	7.2(1.1)	100(0.0)
Young Conifer/ Intense Burn	4	0(0.0)	327(85.6)	0.36(0.05)	1.6(0.5)	4.0(0.8)	100(0.0)
Conifer/ Moderate Burn	7	13(7.0)	2,070(1142.5)	0.39(0.07)	10.0(4.7)	5.9(2.1)	97(1.5)
Conifer/ Light Burn	12	200(109.1)	1,495(457.2)	0.42(0.08)	7.6(2.1)	1.4(0.2)	77(5.7)

in Tables 3 and 4. Additional detail regarding understory plant species abundance and frequency are provided in Appendix A.

Unburned Types

A gradient of overstory canopy cover existed among the unburned types. However, tree density, tree basal area, average dbh, slope, aspect and elevation were variable within types. Non-deciduous overstory cover was lowest (0-5%) in the rough fescue/grassland and logged Douglas-fir seed tree types, and highest in the mature ponderosa pine and mature Douglas-fir types (Table 2). The highest mean overstory cover for any segment sampled was 76% in the mature Douglas-fir type. Segments with high numbers of conifers >38 cm dbh tended to have the greatest overstory canopy cover (Table 2). Overstory canopy cover estimates of <35% described over 70% of the total unburned distance sampled in forested types.

Aspen and spruce types were typically observed on flat sites while mature Douglas-fir and Douglas-fir/larch pole stands were found on steep sites. Subalpine fir types were characteristic of high elevation north aspects and ponderosa pine types occurred on the lowest southwest aspects (Table 2).

Definitive patterns reflecting increased understory structure complexity with decreased overstory canopy were

Table 4. Burn characteristics of 5 vegetation types that burned in the October 1991 BCWMA wildfire.

	Grassland (n=15)	Conifer Light-Burn (n=12)	Conifer Moderate-Burn (n=7)	Young Conifer Intense-Burn (n=4)	Cutover Conifer Intense-Burn (n=20)
Post-Burn Litter Classes	% of stands	% of stands	% of stands	% of stands	% of stands
1. No litter remaining	0	0	0	0	5
2. <1% litter remaining	0	0	13	0	45
3. 1-10% litter remaining	0	17	29	50	40
4. 11-30% litter remaining	0	17	29	25	5
5. 31-50% litter remaining	47	8	29	25	5
6. 51-75% litter remaining	13	33	0	0	0
7. 76-100% litter remaining	40	25	0	0	0
Post-Burn Tree Canopy Classes	% of stands	% of stands	% of stands	% of stands	% of stands
1. All green crowns.	0	0	0	0	0
2. <50% of trees with scorched lower limbs (<3 m high).	0	27	0	0	0
3. 50-100% of trees with scorched lower limbs (<3 m high) and <50% crown loss.	83	73	43	0	0
4. All trees brown or dead with 50-100% crown loss.	17	0	57	50	60
5. 100% crown loss.	0	0	0	50	40
Burn Depth Classes[a]	% of stands	% of stands	% of stands	% of stands	% of stands
1. Unburned	0	0	0	0	0
2. Light ground char	100	100	29	0	0
3. Moderate ground char	0	0	57	75	60
4. Deep ground char	0	0	14	25	40

a = described by Ryan and Noste (1985).

not observed (Tables 2 and 3). Stand types with the greatest shrub layer development were found on flat mesic sites and poor shrub development was characteristic of grassland and ponderosa pine types. Stands of the mature Douglas-fir type had high shrub canopy densities; however, mean shrub heights were low which contributed to relatively low biomass values (Table 3).

Differences in overstory and understory species composition were generally subtle. Major differences among types were structural and topographic. Understory species composition was most similar in grassland and ponderosa pine types; Douglas-fir, spruce and aspen types; and subalpine fir and mixed conifer types (Table 1).

Burned Types

In the burn classification, high canopy cover, percentage of live trees, shrub density, shrub biomass and low charred snag estimates were observed when burn intensities were low (Tables 2 and 3). Similarly, there was high remaining litter, high crown retention and less severe ground char when types burned less intensely (Table 4). The apparent pattern of increased tree density (stems/ha) with reduced burn intensity (Table 2) is biased due to post-burn salvage logging that substantially reduced the number of trees observed in the cutover conifer type.

Overstory canopy cover means ranged from 2% in the grassland type to 18% in the conifer/light burn type (Table 2). Many of the forested stands that had pre-burn cover estimates of 20-40% had post-burn estimates of 0-5%. Overstory canopy cover capable of snow interception in the burn types was extremely limited during 1992 and 1993.

Over 90% of the distance sampled in most burned stands had burned (Table 3). Palatable browse and herbaceous forage across the burn was generally unavailable during the winter of 1992. In winter 1993, herbaceous cover on moderate and intensively burned conifer types was sparse, and total biomass was presumably below pre-burn conditions. Shrubs in these types sprouted well during the growing season following the burn; however, low growing sprouts were unavailable in areas with deep snow. The herbaceous forage of the grassland type responded during the 1992 growing season and grass forage was available during winter 1993.

DISCUSSION

I described 15 unburned and 5 burned vegetation types. The delineation of these types was an attempt to group stands based upon ecological similarity in order to accurately reflect their differential winter use by cervids. The methods employed were designed to obtain large amounts of data specific to established transect routes.

Overstory and understory structural attributes of most unburned and burned forested stands were influenced by past or recent logging activity (Hurley 1994). Logging was the primary reason for the open nature of most overstory canopies. Variability in the abundance of coniferous regeneration and shrubs was presumably due to differences in treatment types (fire and logging), time since treatment, site productivity and past use by elk, MD and WTD. In general, overstory canopy was probably too open to substantially reduce coniferous regeneration and shrubs in forest understories. Managed Douglas-fir stands with multi-storied canopies were also heavily influenced by spruce budworm (*Choristoneura fumiferana*). This infestation was widespread and resulted in the partial defoliation of Douglas-fir seedling/sapling understories.

Topographic relief was minimal and was not considered in the North Fork of the Flathead River study (Jenkins and Wright 1988). In contrast, slope and aspect played a large role in influencing community types on the BCWMA. Elevation probably influenced vegetation to a lesser extent, so it was included as descriptive information for classifications.

A non-characteristic understory species grouping was observed within the conifer/light burn type (Table 1). This was a result of the grouping based on light burn intensity. Stands burning at low intensities with abundant live trees were typically dominated by mature ponderosa pine, mature Douglas-fir, aspen or marsh vegetation with differing characteristic understories.

CHAPTER II: USE OF FORAGE, HABITATS AND SPACE, AND RESOURCE-USE OVERLAP AMONG ELK, MULE DEER AND WHITE-TAILED DEER

INTRODUCTION

The forest and grassland communities of the BCWMA provided winter range for high densities of elk, WTD and MD during this study. Managers were concerned that a combination of high cervid numbers, reduced forage abundance, non-coordinated timber harvesting and harsh winters might lead to excessive elk or deer mortality. This portion of the study was initiated to document the extent, monthly variability and mechanisms of dietary, habitat and spatial overlap among elk, MD and WTD wintering on the BCWMA.

Specific objectives of this portion of the study were to:

1. Estimate relative population levels and winter mortality for elk, MD and WTD.
2. Document the use of forage, habitats and space by the three cervid populations, and estimate the degree of resource-use overlap.
3. Investigate the influence of winter weather conditions on habitat use by the 3 cervid species.

METHODS

Cervid Counts, Recruitment and Winter Mortality

Systematic aerial counts were conducted by MDFWP using a Bell 47-G helicopter in January or early February during 1991-1993. The entire study area was surveyed within a 2-3 day period. Cervids were counted and classified by species, age class and sex. All elk and deer locations were plotted according to group size on 1:24,000 USGS topographic maps in 1992 and 1993. These observations were used to supplement ground observations made during the study. Elk population estimates were calculated following the sightability methods of Samuel et al. (1987), as modified by Unsworth et al. (1991).

Winter mortality in 1992 and 1993 was estimated by counting all dead elk and deer found within 50 m of the transects described in Chapter 1. Transects were surveyed at 2-week intervals. Eleven days were required to survey the 40 km route. Species, location, estimated carcass age and date were recorded for all observed mortalities. When possible, age was determined by tooth replacement and wear (Severinghaus 1949), and nutritional condition was estimated through visual examination of femur marrow (Cheatum 1949). Mortality estimates were reported as the number of dead elk and deer per km^2. Incidental observations of dead elk and deer were documented during daily operations from January-

April 1992-1993. Observations of road-killed elk and deer on Highway 200 (between Clearwater Junction and the Woodworth road) were also recorded.

Forage Use and Dietary Overlap

Forage use and dietary overlap among cervids were determined using microhistological analyses of composited fecal samples (Sparks and Malechek 1968). Monthly composites consisted of approximately 3 g of material from each of 16-66 ($\bar{x}$ = 31) fresh pellet groups that were collected for each species during winter (January, February, March) 1992 and 1993. Additional winter (January - March combined) composites for 1992 and 1993 were constructed in the same manner from 48-126 ($\bar{x}$ = 71) fresh pellet groups. To verify species, deer samples were collected from individuals that were backtracked or observed defecating. Pellets were consistently collected from a variety of sites and habitats and were frozen within 8 hours of collection.

Three additional composites were made from pellet groups (66 elk, 93 MD and 98 WTD) deposited during an extremely mild weather period in January 1994. Temperatures were unseasonably warm and very little snow cover existed on the study area. These samples were collected for comparing winter diets during optimum foraging conditions (January 1994) with those representing more typical snow conditions (January 1993).

Fecal samples were analyzed by personnel at the Wildlife Habitat Laboratory, Washington State University, Pullman, following the procedures of Davitt and Nelson (1980). Diet forage composition was expressed as the percent cover of epidermal plant species fragments in 200 random microscope fields.

Dietary overlap was calculated using Morisita's (1959) coefficient as modified by Horn (1966):

$$C_\lambda = [\ 2 \sum_{i=1}^{s} P_{ij} \cdot P_{ik}\ ] \div [\ \sum_{i=1}^{s} P_{ij}^2 + \sum_{i=1}^{s} P_{ik}^2\ ]$$

where C_λ = the mutual overlap between cervid species j and k, and P_{ij} and P_{ik} = the proportion of use of resource category i by cervid species j and k respectively, and s = the number of resource categories. The overlap coefficient varies from 0.0 when resource use is distinct to 1.0 when it is identical. Overlap indices did not provide statistical inferences about ecological relationships; however, they did provide measures of ecological similarity.

Relative importance indices were calculated to rank the forage values of plant species on the winter range under current cervid densities. These indices were calculated as the frequency of a plant's use in 18 diets (6 elk, 6 MD, 6 WTD) times the summed percentage consumed for winters 1992 and 1993. Indices were expressed as a percentage of all plant species observed in elk and deer diets.

Habitat and Spatial Use and Overlap

Habitat use and spatial distribution were examined from 1 January - 10 March 1992-1993 by recording all observations of animals and tracks along the 5 transects described in Chapter 1 (Fig. 4). All transects were surveyed on foot every 13-15 days. All observations of track sets that intercepted the transects and cervid groups were recorded. The sampling interval assured that 4 counts along 40 km of transects were obtained each winter (160 km winter total) and that cervids had an opportunity to redistribute during the interval.

All track sets were recorded to avoid bias from judging fresh tracks. Tracks were obliterated along each route to avoid recounting during subsequent surveys. Individual trails made by several animals were counted as single track sets.

Cervid track densities (tracks/km of transect) were compared among 20 habitat categories (Tables 1-4) and 4 spatial zones for January and February 1992 and 1993. Spatial zone boundaries were based on mapped cervid observations recorded during the winters of 1991-1993. Track densities were converted to track proportions (use), and compared with transect distance proportions for habitat and spatial categories (availability). Use-availability comparisons were based on the methods of Marcum and

Loftsgaarden (1980), but were modified so that:

$$(P_{1A} - P_{2Ai}) \pm Z \cdot [P_{1A}(1-P_{1A})/n_1 + P_{2Ai}(1-P_{2Ai})/n_{2i}]^{1/2}$$

where n_1 = total number of segments (stands) sampled (n = 191), P_{1A} = proportion of distance surveyed in category A, n_{2i} = total number of tracks counted for species i, P_{2Ai} = proportion of tracks counted for species i in category A, and Z = the Z value for a selected percentile for a standard normal distribution. Simultaneous 90% confidence intervals (α = 0.1) were used to test for significant differences among the 20 vegetation types because of the large number of categories (Marcum and Loftsgaarden 1980). Simultaneous 95% confidence intervals (α = 0.05) were used to test for significant differences in use among the 4 spatial zones. Resource-use overlap indices (Horn 1966) (same as page 35) were used to evaluate the degree of monthly habitat and spatial overlap among pairs of cervid species.

Deer Track Estimates

MD and WTD tracks could not be differentiated in the field. Therefore, numbers of MD and WTD tracks were estimated from proportions of deer species observations along transects. A deer species was assumed to make tracks in a given habitat in relative proportion to its observed proportion in that habitat. Singer (1979) described a similar technique where tracks and observations were given equal weight as use indicators for moose, elk and WTD. Group sizes were not included in use estimates during Singer's (1979) study.

Group sizes of observed deer were considered for estimating MD and WTD track proportions from observations. This was done because use of a category by 28 MD for 1 day was assumed to be relatively equal to use by 1 MD for 28 days. Group sizes would also more accurately measure use by species that consistently occur in large groups.

Species, group size and distance from observer were recorded for all sightings of deer within 200 m of the investigator during track counts. Distance estimates were attempted using a portable range-finder, but were determined to be less accurate than visual estimates and too time consuming; thus distances were visually estimated. Observations of MD and WTD mapped during helicopter surveys and daily field operations were used to supplement transect observations.

Deer track estimates were determined by calculating proportions of monthly MD and WTD observations for deer observed within 200 m of each transect segment. Deer observations were frequently linked to more than one segment (i.e., deer observed within 200 m of a segment endpoint were assigned to both adjoining segments). Segments with tracks, but no deer sightings within 200 m, were assigned the average proportion of 2 adjacent segments or average proportion of the 5 nearest observations. Proportions of sightings of MD and WTD by segment were multiplied by the total monthly segment deer track count. This yielded monthly MD and WTD track estimates by segment.

Monthly MD and WTD track estimates for each segment were summed within habitat and spatial categories. Track totals for each category were converted to tracks/km and proportions for use-availability analysis.

To accept the hypothesis that deer tracks crossing transects were proportional to deer species sighted, I assumed that MD and WTD were equally observable in like habitats (i.e., no behavioral, body size, coloration or group size differences existed that would bias observation results). It would be difficult to evaluate the magnitude of potential observation bias. However, most factors that would increase observation bias would also effect distance-from-observer estimates for the 2 deer species. Therefore, distance-from-observer means were calculated from 1992-1993 observation data. Student's two-sided *t*-test with pooled variance estimate (Norusis 1988) was used to test for differences in the means of distances observed for MD and WTD.

Radio Telemetry

Elk, MD and WTD deer were captured in corral traps, collapsible Clover traps (Thompson et al. 1989) and non-collapsible Clover traps (Clover 1956). All elk and deer were marked with metal eartags, and aged by tooth wear and replacement (Severinghaus 1949, Greer and Yeager 1967). Six elk (3 males and 3 females), 11 female MD and 10 female WTD were fitted with radio transmitters during the winter of 1991. Only distributions for adult females were examined. Two female elk radio-collared during prior research (Hurley 1994) were also monitored. Elk, MD and WTD that were not radioed were fitted with metal ear tags and individually marked rubber neckbands (females), or numbered livestock eartags (males). Observations of marked animals supplemented other distribution data.

From 2-7 radio-collared individuals of each species were relocated from the ground or from aircraft 3-6 times per month from January-February 1992 and 1993. Aerial relocations were obtained from a Citabria aircraft with a single belly-mount rotational antenna. Ground relocations were obtained using a minimum of 3 mapped triangulation bearings or independent visual observations (White and Garrot 1986). Relocations were classified for accuracy as exact (visual), within 100 m, and within 200 m. Radio-relocations with accuracy estimates >200 m were omitted. Radio-collars placed at known locations, shed collars, and collars from dead animals were used to determine ground and aerial relocation accuracy.

Universal Transverse Mercator (UTM) coordinates were assigned to each relocation point. UTMs were entered into the Pamap Geographic Information System (GIS) software package as point data for individual minimum convex polygons. Monthly minimum convex polygons for radio-collared elk, MD and WTD were digitized on individual levels and polygon areas (km^2) were determined. Individual vector levels were combined and overlaid on a raster layer that displayed relative overstory canopy closure described by DelSordo (1993). More rigorous analyses of telemetry data were not attempted because of small sample sizes.

Winter Weather Conditions

Weather data were collected during the winters of 1992 and 1993. Twenty snow measurement locations were selected, which were comprised of diverse combinations of overstory canopy cover, slope, aspect and elevation. Snow measurement locations were surveyed once per week at varied times of day (from 1000 to 1500 hours).

Methods for calculating mobility resistance, snow severity, and winter severity indices are given in Appendix B. Averages of 5 mobility resistance and 5 snow depth measurements (cm) were recorded for each location. Temperature was measured at 6 locations that had high site variability. Mean mobility resistance indices, snow depths and snow severity indices were calculated for the 20 locations for 1992 and 1993. Average winter severity indices (a function of mobility resistance, snow depth and temperature) were calculated for the 6 locations where temperature was measured.

To estimate the direct influence of snow conditions on cervid distributions, additional snow depth measurements were recorded at 10 evenly spaced points along each transect segment during track surveys. Additional mobility resistance measurements were recorded (10 per segment) during track surveys in 1993. Means for snow depth and mobility resistance were calculated for each segment. The influence of snow on cervid distribution was evaluated by comparing percentages of cervid tracks with percentages of distance surveyed in 4 snow depth and 4 mobility resistance classes (Marcum and Loftsgaarden 1980).

RESULTS

Cervid Counts, Recruitment and Winter Mortality

Thirteen of 63 marked MD (21%), and 1 of 24 marked WTD (4%) were observed during the 1991 aerial count. Actual numbers of marked elk at the time of the survey were unknown. Deer were difficult to count during aerial surveys due to scattering behavior and affinities for forested habitats. Elk were easier to observe and count because of their size, coloration and grouping behavior.

Numbers for all three species remained relatively stable during the study (Table 5.A.). Counts of approximately 1,000 elk, 600 MD and 200 WTD were normally obtained. However, low proportions of marked MD and WTD observed in the 1991 aerial survey indicated that observability of deer was low; thus counts were probably quite conservative.

Three-year recruitment (calves/100 cows and fawns/100 adults) means calculated from aerial survey estimates on the BCWMA were slightly greater than those obtained for Region-wide estimates (MDFWP, Region 2) for the same years (Table 5.B).

Carcass densities observed during transect surveys were low ($<1/km^2$) for all 3 cervid species in 1992 and 1993 (Table 6.A). However, slight increases in carcasses were observed for MD and WTD in 1993. Percentage mortality estimates for elk and deer aerial counts, as calculated from carcass densities extrapolated across the study area, were <14% for all 3 cervid species in 1992, and all but WTD (32.7%) in 1993.

Predation and vehicles were the greatest known mortality factors on winter range (Table 6.B). Mortality resulting from malnutrition was the lowest known factor for all 3 species (Table 6.B). However, some carcasses in the unknown category may also have died from malnutrition. Mortality of the 0.5 year age class from hunting could not

Table 5.A. Winter aerial elk sightability estimates (Samuel et al. 1987) and deer counts for the BCWMA during 1991-93.

8-9 February 1991

Species	Total[b]	Juveniles/100 Adults[a]
Elk	990 (± 36)	30
MD	575	53
WTD	233	49

8-9 January 1992

Species	Total[b]	Juveniles/100 Adults[a]
Elk	384 (± 46)[c]	32
MD	669	64
WTD	257	48

2-4 February 1993

Species	Total[b]	Juveniles/100 Adults[a]
Elk	935 (± 40)	46
MD	648	73
WTD	201	66

a = elk ratios are for calves/100 cows.
b = ± 90% confidence bounds for sightability estimates in parentheses.
c = An October 1991 wildfire caused a redistribution of elk to adjacent areas outside of HD 282 and is reflected in the 1992 survey results.

Table 5.B. Recruitment (calves/100 cows and fawns/100 adults) means calculated from 1991-1993 classification estimates obtained for the BCWMA and MDFWP Region 2 (Region Two Deer and Elk Survey and Inventory Tables, 1 July 1993 - 30 June 1994, MDFWP, unpubl. data).

	BCWMA		Region 2	
	$\bar{x}$	SE	$\bar{x}$	SE
Elk	36.0	5.0	33.3	1.8
MD	63.3	5.7	54.7	1.5
WTD	54.1	5.7	50.7	3.0

Table 6.A-D. Mortality summary for the BCWMA.

A. Mortalities observed /km^2 (and n) along track transects from January-April 1992 and 1993.

Species	1992	1993
Elk	0.49(2)	0.00(0)
MD	0.73(3)	0.98(4)
WTD	0.24(1)	0.73(3)
Survey Area (square km)	4.09	4.09

B. Percent non-hunting winter mortality sources for carcasses found from January to April 1992-1993.

Species	n	Road Kills	Predation	Malnutrition	Unknown
Elk	13	7.7	30.8	7.7	53.8
MD	54	61.1	14.8	1.9	22.2
WTD	22	63.6	13.7	0	22.7

C. Percent non-hunting winter mortality by age and sex for carcasses found from January-April 1992 and 1993.

		Age (years)							Sex		
Species	n	0.5	1.5	2.5	3.5	4.5	5.5	6.5+	n	Male	Female
Elk	12	58.3	16.7	16.7	8.3	0.0	0.0	0.0	11	63.6	36.4
MD	46	58.7	15.2	6.5	2.2	2.2	2.2	13.0	38	28.9	71.1
WTD	12	75.0	0.0	8.3	0.0	0.0	0.0	16.7	11	27.3	72.7

D. Percent marked animal hunting mortality by age and sex for fall 1991 and fall 1992 combined.

		Age (years)						Sex	
Species	n	1.5	2.5	3.5	4.5	5.5	6.5+	Male	Female
Elk	18	7.1	21.4	7.1	7.1	14.3	42.9	16.7	83.3
MD	10	40.0	30.0	10.0	0.0	0.0	20.0	90.0	10.0
WTD	3	0.0	33.3	0.0	33.3	0.0	33.3	66.7	33.3

be evaluated because juveniles were not marked prior to the hunting season. Non-hunting winter mortality of elk, MD and WTD in the 0.5 year age class was greater than for other age classes (Table 6.C). Male elk and female deer appeared to be most vulnerable to non-hunting mortality. Hunting mortality was greater for marked female elk, and male deer of both species (Table 6.D).

Forage Use

Cervid diets in winter varied monthly within years, and varied in the same months between years (Figs. 6 and 7). Elk and WTD winter diets (3 months combined) varied less between years than MD diets (Fig. 8). Monthly winter diets of elk during 1992 and 1993 were dominated by graminoids, whereas diets of MD and WTD were dominated by conifers (Figs. 6 and 7). Elk use of forbs, deciduous shrubs, evergreen shrubs and conifers varied within years and between years; however, graminoid use remained relatively high and constant (Figs. 6 and 7). Evergreen shrubs received greater use in late winter by all cervids. Forage species of particular importance for elk during both winters were rough fescue and elk sedge, whereas Douglas-fir, ponderosa pine and Oregon grape were species found in greatest abundance in MD and WTD diets (Appendices C and D).

Conifers and graminoids had the highest overall forage importance estimates for the 3 cervid species during winter,

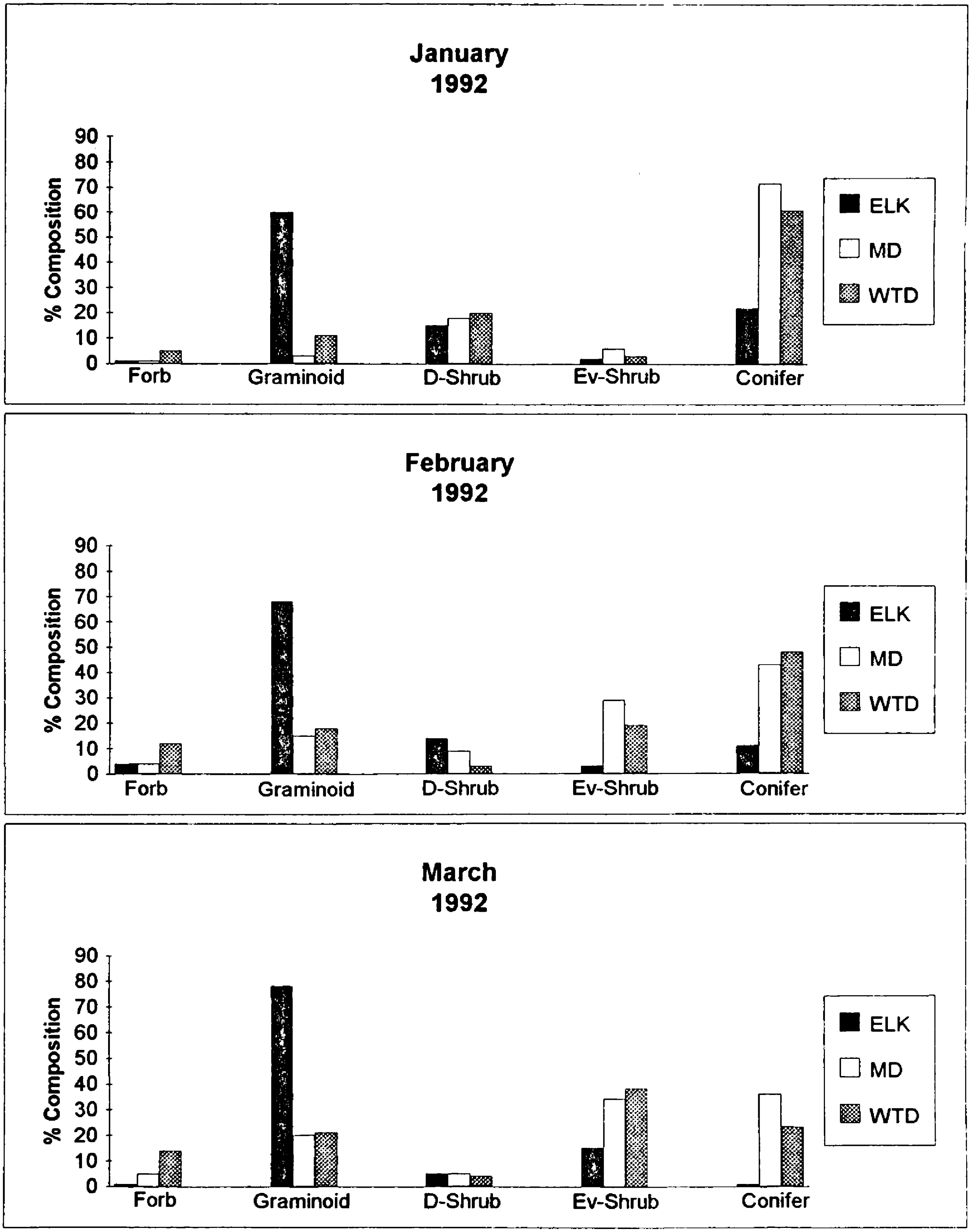


Figure 6. Composition of forbs, graminoids, deciduous shrubs (D-Shrub), evergreen shrubs (Ev-Shrub) and conifers in the diets of elk, mule deer and white-tailed deer on the BCWMA during winter 1992.

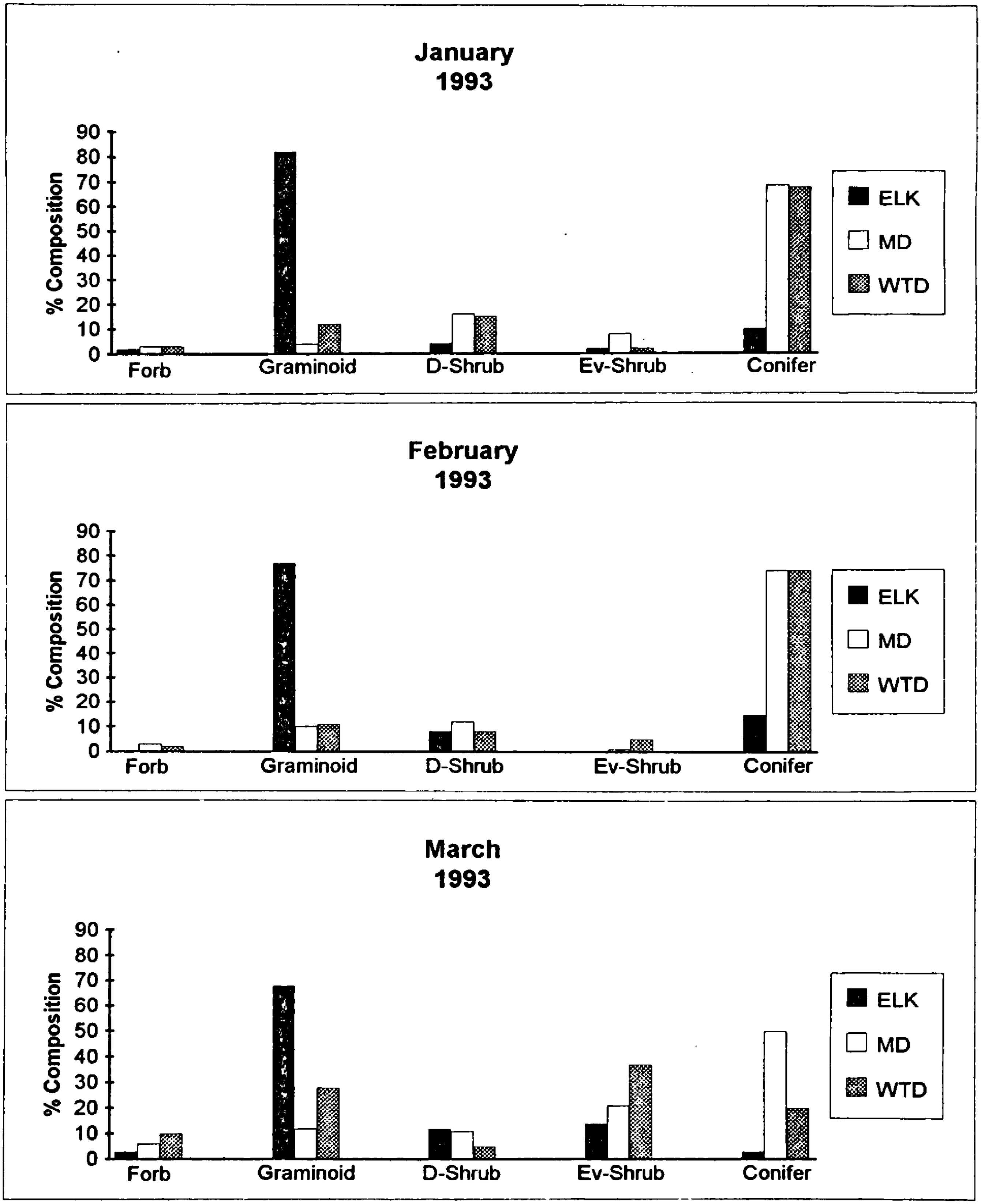
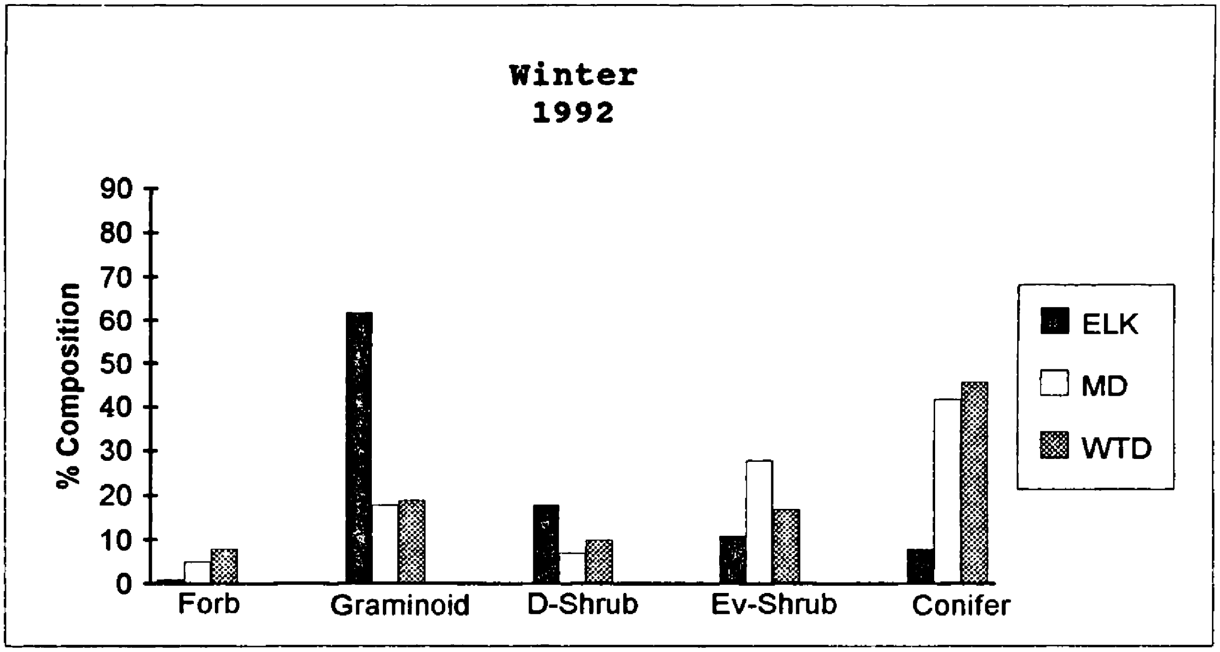


Figure 7. Composition of forbs, graminoids, deciduous shrubs (D-Shrub), evergreen shrubs (Ev-Shrub) and conifers in the diets of elk, mule deer and white-tailed deer on the BCWMA during winter 1993.



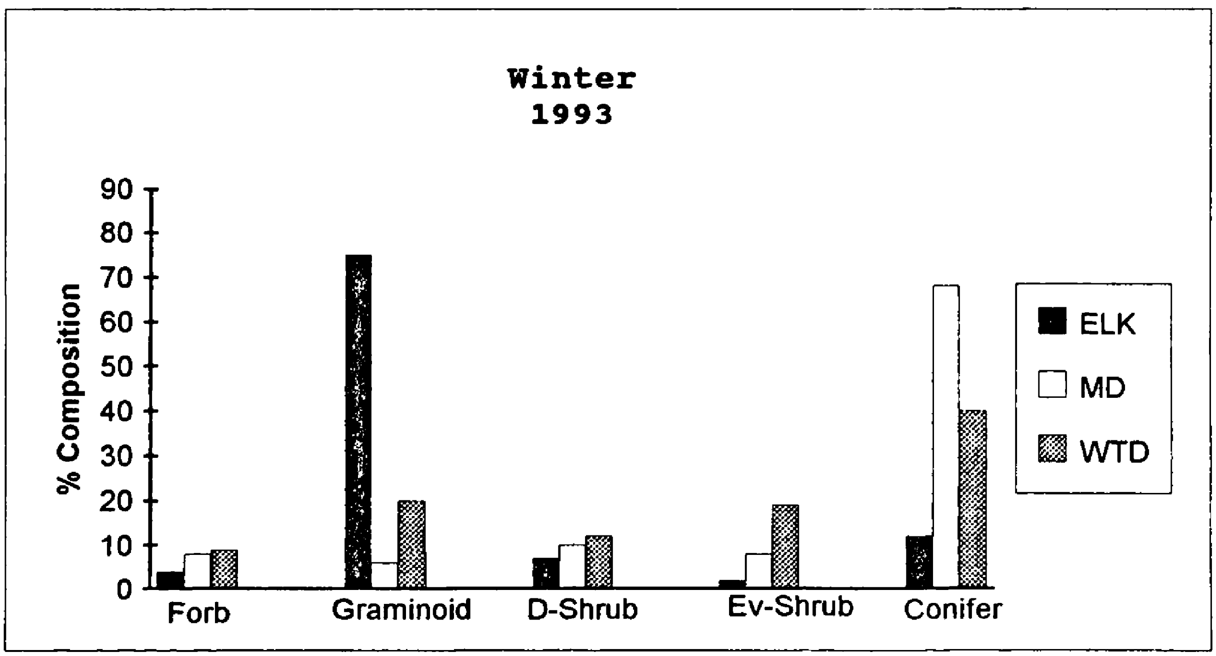


Figure 8. Composition of forbs, graminoids, deciduous shrubs (D-Shrub), evergreen shrubs (Ev-Shrub) and conifers in the diets of elk, mule deer and white-tailed deer on the BCWMA during the winters (January, February and March combined) of 1992 and 1993.

and forbs had the lowest (Table 7). Douglas-fir and rough fescue had the highest importance ratings for the conifer and graminoid classes respectively. Shrubs that received the most use were Oregon grape and serviceberry (Table 7).

From field observations, tree lichen (Alectoria spp.) was the most frequently consumed forage item for all cervids using forested habitats. However, lichen was poorly represented in fecal pellets. Lichen was probably under-represented in pellet samples because of its high digestibility, and destruction by bleach during slide preparations (B. B. Davitt, Wash. State Univ., pers. commun.).

As winter progressed in 1992, elk, MD and WTD use of graminoids and evergreen shrubs increased, whereas deciduous shrub and conifer use generally decreased (Fig. 6 and Appendix C). Both deer species also increased their use of forbs as winter progressed in 1992 (Fig. 6 and Appendix C).

Trends for 1993 were less apparent (Fig. 7 and Appendix D). Elk use of graminoids slightly decreased, whereas MD and WTD graminoid use increased throughout winter 1993 (Fig. 7). Elk use of deciduous shrubs increased, while MD use remained relatively constant, and WTD use decreased (Fig. 7). Conifer use by all 3 cervids in 1993 was greatest in February and was lowest in March. However, conifers remained the dominant forage for MD in March 1993 (Fig. 7). The greatest monthly shifts in use of forage types by

Table 7. Winter range forage importance indices expressed as percent relative importance of plants consumed by elk, mule deer and white-tailed deer. Indices are based on frequency of use and abundance in the 3 cervid diets combined for winters of 1992 and 1993. Plants with index values <0.1 were observed in trace amounts (denoted by T).

Common Name	Forage Taxon	% Relative Importance
Forbs		
Arrowleaf Balsamroot	*Balsamorhiza sagittata*	1.3
Other Forbs	Other Forbs	1.1
Lupines	*Lupinus spp.*	0.3
Indian Paintbrush	*Castilleja spp.*	T
Spotted Knapweed	*Centaurea maculosa*	T
Blue Bells	*Mertensia spp.*	T
Common Yarrow	*Achillea millefolium*	T
Pussy-toes	*Antennaria spp.*	T
Arnica	*Arnica spp.*	T
Aster	*Aster spp*	T
Musk/Canada Thistles	*Cirsium spp.*	T
Horse Tail	*Equisetum spp.*	T
Wild Strawberry	*Fragaria virginiana*	T
Bedstraw	*Galium boreale*	T
Mustards	*Brassicaceae Family*	T
Wooly Mullein	*Verbascum thapsus*	T
Subtotal		2.7
Graminoids		
Rough Fescue	*Festuca scabrella*	10.8
Elk Sedge (primarily)	*Carex spp.*	9.4
Bluegrass	*Poa spp.*	3.6
Needlegrass	*Stipa spp.*	2.6
Idaho Fescue	*Festuca idahoensis*	2.5
Prairie Junegrass	*Koeleria cristata*	0.8
Other Wheatgrass	*Agropyron spp.*	0.5
Bluebunch Wheatgrass	*Agropyron spicatum*	0.5
Brome	*Bromus spp.*	0.5
Bentgrass/Red top	*Agrostis spp.*	0.2
Other Grass	Other Grass	0.2
Pine Grass	*Calamagrostis rubescens*	0.2
Timothy	*Phleum pratense*	0.1
Wild Rye	*Elymus glaucus*	0.1
Orchard Grass	*Dactylis glomerata*	T
Foxtail Barley	*Hordeum jubatum*	T
Other Fescue	*Festuca spp.*	T
Subtotal		32.1

Table 7. continued

Deciduous Shrubs		
Serviceberry	*Amelanchier alnifolia*	4.3
Upland Willow	*Salix scouleriana*	3.3
Other Shrubs	Other Shrubs	0.3
Rocky Mountain Maple	*Acer glabrum*	0.2
Buffaloberry	*Shepherdia canadensis*	0.1
Hawthorn	*Cretaegus douglasii*	T
Thimbleberry	*Rubus parviflorus*	T
Woods Rose	*Rosa woodsii*	T
Water Birch	*Betula occidentalis*	T
Elderberry	*Sambucus spp.*	T
Redozier Dogwood	*Cornus stolonifera*	T
Aspen/Black Cottonwood	*Populus spp.*	T
Chokecherry	*Prunus virginiana*	T
False Huckleberry	*Menziesia ferruginea*	T
Ninebark	*Physocarpus malvaceus*	T
Snowberry	*Symphoricarpos albus*	T
Subtotal		8.3
Evergreen Shrubs		
Oregon Grape	*Berberis repens*	8.5
Current/Gooseberry	*Ribes spp./Berberis repens*	3.3
Shiny-Leaf Ceanothus	*Ceanothus velutinus*	0.1
Green Rabbitbrush	*Chrysothamnus viscidiflorus*	0.1
Bearberry	*Arctostaphylos uva-ursi*	T
Sagebrush	*Artemisia spp.*	T
Subtotal		12.0
Conifers		
Douglas-fir	*Pseudotsuga menziesii*	32.6
Ponderosa Pine	*Pinus ponderosa*	9.9
Conifer Bark	Conifer Bark	2.0
Juniper	*Juniperus scopulorum*	0.2
Subalpine Fir	*Abies lasiocarpa*	T
Western Larch	*Larix occidentalis*	T
Subtotal		44.8
Other		
Tree Lichen	*Alectoria spp.*	0.1
Moss	Moss	T
Composite Family	*Asteraceae*	T
Subtotal		0.1

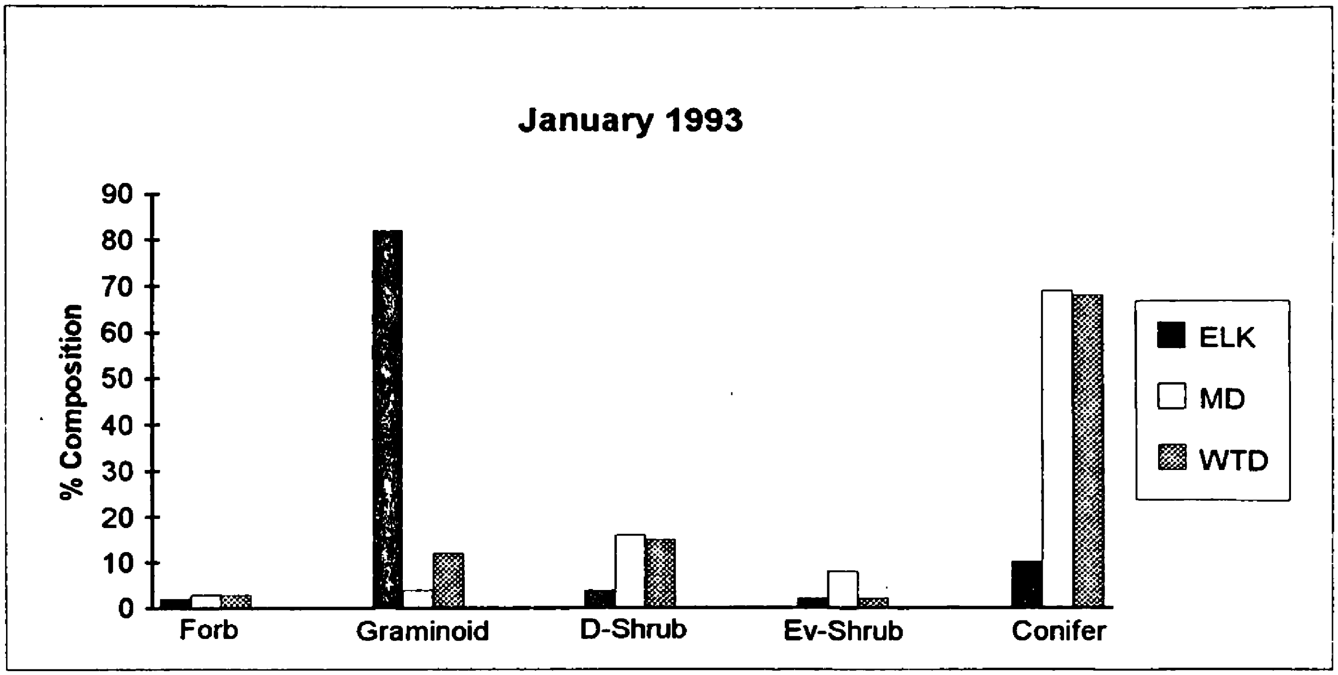
cervids were observed in the graminoid, evergreen shrub and conifer types.

Elk diets from the extremely mild January of 1994 were similar to diets sampled in the more typical January of 1993 (Fig. 9). In January 1994, MD and WTD diets were lower in conifers and deciduous shrubs, and substantially higher in evergreen shrubs and forbs (Fig. 9). Although snow cover was sparse and availability of all forage types was high in the January 1994 sample, conifer was a substantial component of MD diets and remained the dominant forage type used by WTD (Fig. 9).

Habitat and Spatial Use

Habitat selection and spatial distribution were estimated from 61,671 total track sets counted during 8 transect surveys. Habitat use by elk, MD and WTD varied across months within both years, and within months across years (Tables 8 and 9).

Elk used the ponderosa pine, aspen and Douglas-fir/open vegetation types significantly greater than availability, but used the cutover conifer/intense burn type significantly less than availability in 1992 (Table 8). In January 1993 elk used Douglas-fir/open and burned grassland greater than availability. However, they used rough fescue/grassland, aspen, and Douglas-fir/open types greater than availability in February 1993 (Table 9). During January and February of



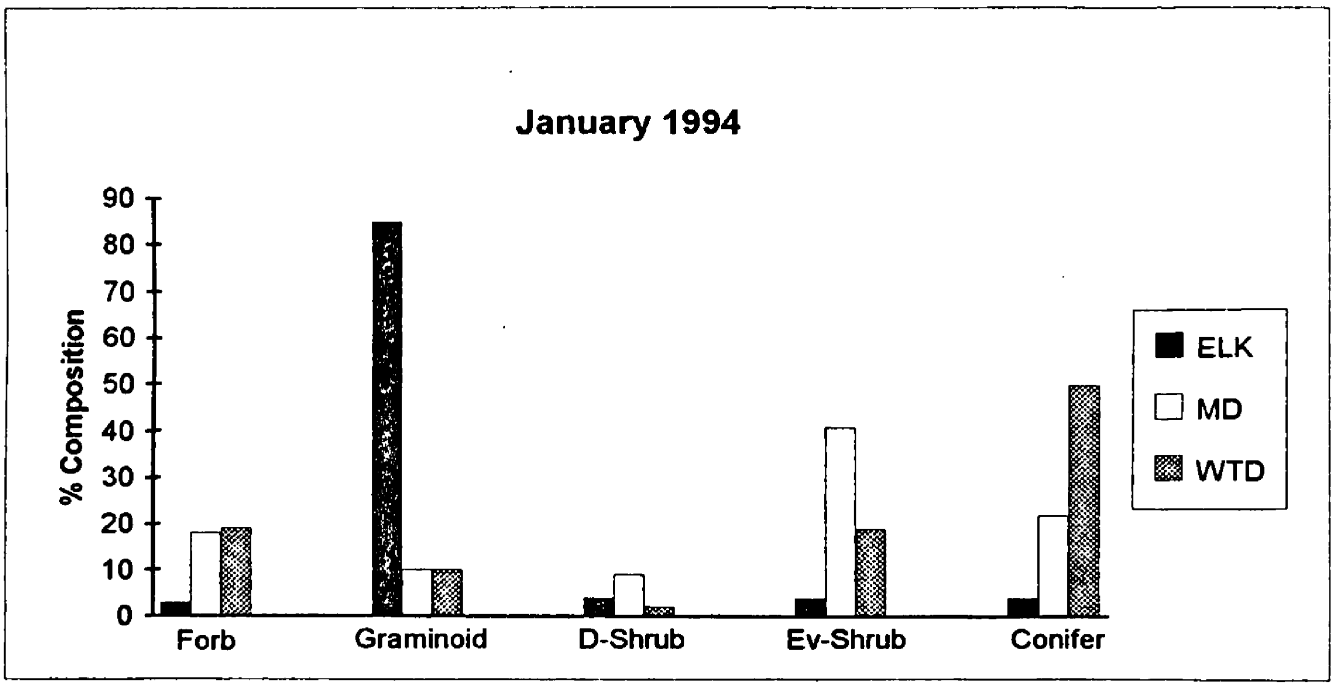


Figure 9. Composition of forbs, graminoids, deciduous shrubs (D-Shrub), evergreen shrubs (Ev-Shrub), and conifers in the diets of elk, mule deer and white-tailed deer during conditions of low forage availability (January 1993) and high forage availability (January 1994) on the BCWMA.

Table 8. Monthly cervid track counts (tks) compared to survey distance (Dis) in 20 habitat categories on the BCWMA during 1992. Use-availability (ua) symbols indicate use significantly greater than availability (+), use significantly less than availability (-) and use not significantly different (o) based on Bonferroni confidence intervals ($P < 0.10$, Marcum and Loftsgaarden 1980). Refer to Chapter 1, Tables 1-4 for complete habitat descriptions.

January Habitat	1992 %Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
RF.Grslnd.	3.3	2.7	1.4	(o)	74	0.5	(o)	40	1.3	(o)	70
DF-seed tr.	3.4	2.7	1.0	(o)	54	2.7	(o)	226	0.1	(o)	3
Aspen	2.2	1.8	5.5	(+)	287	3.2	(o)	265	0.5	(o)	29
P.Pine	5.4	4.3	10.9	(+)	564	0.7	(-)	57	11.0	(+)	595
SA Fir OvR	2.2	1.8	0.4	(o)	21	1.3	(o)	105	0.1	(o)	5
DF-open	9.8	7.9	28.6	(+)	1,487	25.5	(+)	2,113	8.9	(o)	484
DF-xeric	10.6	8.6	5.6	(o)	290	21.7	(+)	1,797	14.6	(o)	793
DF-cool	11.2	9.0	12.8	(o)	666	16.5	(o)	1,370	13.6	(o)	737
Spruce	1.4	1.1	1.5	(o)	78	3.1	(o)	254	3.7	(o)	198
DF-cold	2.6	2.1	1.7	(o)	90	2.5	(o)	205	5.5	(o)	296
SA Fir	0.8	0.7	0.9	(o)	48	4.0	(+)	333	0.0	(o)	0
DF/WL-pole	5.9	4.8	3.3	(o)	171	5.0	(o)	412	15.2	(+)	822
Mixed-con.	1.1	0.9	1.3	(o)	68	0.1	(o)	5	1.4	(o)	74
DF-Mat	3.3	2.7	0.9	(o)	48	6.4	(o)	531	10.9	(+)	589
P.Pine-Mat	2.9	2.3	4.3	(o)	222	0.0	(o)	0	11.4	(+)	618
Bnd Grslnd	12.1	9.8	10.4	(o)	541	0.3	(-)	28	0.9	(-)	50
C-c int bn	9.9	8.0	1.6	(-)	85	0.8	(-)	70	0.0	(-)	0
Y-c int bn	2.1	1.7	0.6	(o)	33	0.2	(o)	17	0.0	(o)	0
Con mod bn	3.9	3.2	1.0	(o)	54	1.4	(o)	118	0.1	(o)	8
Con lt bn	5.7	4.6	6.1	(o)	317	4.0	(o)	331	0.8	(-)	43
Subtotal		80.8			5,198			8,276			5,416

February Habitat	1992 %Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
RF.Grslnd.	3.4	2.5	7.1	(o)	285	0.0	(o)	1	1.4	(o)	48
DF-seed tr.	3.8	2.7	1.3	(o)	51	1.2	(o)	63	0.0	(o)	0
Aspen	2.4	1.7	6.2	(+)	248	1.6	(o)	83	1.0	(o)	36
P.Pine	5.4	3.9	16.2	(+)	654	0.4	(-)	20	16.3	(+)	572
SA Fir OvR	2.5	1.8	0.9	(o)	36	0.2	(o)	8	0.0	(o)	0
DF-open	10.2	7.3	10.7	(o)	430	21.2	(+)	1,086	9.0	(o)	314
DF-xeric	9.7	7.0	12.5	(o)	503	28.7	(+)	1,467	7.3	(o)	257
DF-cool	11.9	8.6	14.9	(o)	601	11.7	(o)	599	5.8	(o)	203
Spruce	1.5	1.1	2.2	(o)	88	1.8	(o)	92	4.3	(+)	150
DF-cold	2.8	2.0	1.2	(o)	48	2.9	(o)	148	5.2	(o)	184
SA Fir	0.9	0.7	0.7	(o)	30	3.7	(+)	191	0.0	(o)	0
DF/WL-pole	6.5	4.7	4.5	(o)	181	7.0	(o)	358	19.4	(+)	682
Mixed-con.	1.2	0.9	1.4	(o)	56	0.5	(o)	26	0.0	(o)	0
DF-Mat	2.8	2.0	1.9	(o)	76	9.0	(+)	458	11.1	(+)	389
P.Pine-Mat	2.6	1.9	4.1	(o)	167	0.4	(o)	20	18.6	(+)	654
Bnd Grslnd	13.0	9.4	8.1	(o)	328	0.2	(-)	9	0.1	(-)	5
C-c int bn	9.4	6.8	0.5	(-)	21	1.5	(-)	78	0.0	(-)	0
Y-c int bn	2.3	1.6	0.7	(o)	28	0.0	(o)	1	0.0	(o)	0
Con mod bn	3.1	2.3	1.4	(o)	55	1.9	(o)	96	0.0	(o)	0
Con lt bn	4.5	3.3	3.6	(o)	146	6.1	(o)	315	0.4	(o)	15
Subtotal		72.2			4,032			5,117			3,510

Table 9. Monthly cervid track counts (tks) compared to survey distance (Dis) in 20 habitat categories on the BCWMA during 1993. Use-availability (ua) symbols indicate use significantly greater than availability (+), use significantly less than availability (-), and use not significantly different (o) based on Bonferroni confidence intervals (P < 0.10, Marcum and Loftsgaarden 1980). Refer to Chapter 1, Tables 1-4 for complete habitat descriptions. Habitat abbreviations and corresponding vegetation types are the same as those given in Table 8.

January Habitat	1993 %Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
RF.Grslnd.	3.3	2.7	3.4	(o)	231	0.5	(o)	30	0.3	(o)	13
DF-seed tr.	3.4	2.8	1.0	(o)	70	2.1	(o)	118	0.0	(o)	2
Aspen	2.2	1.8	3.2	(o)	220	2.6	(o)	148	0.8	(o)	31
P.Pine	5.3	4.3	2.5	(o)	172	0.9	(o)	50	8.4	(o)	316
SA Fir OvR	2.2	1.8	0.2	(o)	15	0.2	(o)	12	0.0	(o)	0
DF-open	9.8	8.0	16.3	(+)	1,109	21.6	(+)	1,242	7.9	(o)	297
DF-xeric	10.6	8.6	4.9	(o)	332	20.3	(+)	1,171	7.7	(o)	288
DF-cool	11.2	9.1	10.7	(o)	731	17.7	(o)	1,017	19.0	(+)	711
Spruce	1.4	1.1	1.4	(o)	93	1.8	(o)	105	4.5	(+)	170
DF-cold	2.6	2.1	1.7	(o)	119	4.1	(o)	237	6.1	(+)	227
SA Fir	0.8	0.7	0.4	(o)	29	1.2	(o)	69	0.0	(o)	0
DF/WL-pole	5.9	4.8	1.5	(o)	101	4.0	(o)	232	14.5	(+)	545
Mixed-con.	1.1	0.9	0.7	(o)	50	1.7	(o)	95	0.6	(o)	23
DF-Mat	3.3	2.7	0.6	(o)	40	5.3	(o)	303	7.8	(+)	292
P.Pine-Mat	2.9	2.4	0.3	(o)	20	0.0	(o)	0	15.2	(+)	570
Bnd Grslnd	12.1	9.8	34.7	(+)	2,359	0.0	(-)	2	0.2	(-)	7
C-c int bn	9.9	8.0	4.7	(o)	320	1.5	(-)	84	1.1	(-)	43
Y-c int bn	2.1	1.7	2.2	(o)	149	0.1	(o)	8	0.0	(o)	0
Con mod bn	4.0	3.2	4.3	(o)	293	6.0	(o)	347	0.0	(-)	0
Con lt bn	5.9	4.7	5.2	(o)	353	8.4	(o)	487	5.6	(o)	211
Subtotal		81.1			6,806			5,759			3,744

February Habitat	1993 %Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
RF.Grslnd.	3.3	2.6	15.4	(+)	959	0.0	(o)	2	0.3	(o)	9
DF-seed tr.	3.4	2.8	0.7	(o)	44	1.8	(o)	79	0.0	(o)	0
Aspen	2.2	1.8	7.5	(+)	468	1.6	(o)	72	0.6	(o)	17
P.Pine	5.4	4.3	6.9	(o)	432	0.2	(-)	11	6.2	(o)	191
SA Fir OvR	2.3	1.8	0.6	(o)	37	0.3	(o)	13	0.0	(o)	0
DF-open	9.9	8.0	16.4	(+)	1,024	21.2	(+)	958	5.5	(o)	170
DF-xeric	10.7	8.6	3.9	(-)	242	22.9	(+)	1,032	10.9	(o)	334
DF-cool	11.3	9.0	9.7	(o)	604	14.4	(o)	648	13.6	(o)	418
Spruce	1.4	1.1	1.7	(o)	108	1.7	(o)	77	4.0	(+)	124
DF-cold	2.6	2.1	0.9	(o)	59	2.5	(o)	114	7.2	(+)	220
SA Fir	0.9	0.7	0.6	(o)	37	4.9	(+)	222	0.0	(o)	0
DF/WL-pole	6.0	4.8	2.2	(o)	140	5.1	(o)	230	23.0	(+)	706
Mixed-con.	1.1	0.9	1.9	(o)	119	0.4	(o)	18	0.0	(o)	0
DF-Mat	3.3	2.7	1.3	(o)	81	8.2	(+)	371	15.6	(+)	478
P.Pine-Mat	2.9	2.4	1.3	(o)	79	0.0	(o)	0	12.8	(+)	392
Bnd Grslnd	12.0	9.7	14.4	(o)	897	0.1	(-)	3	0.0	(-)	0
C-c int bn	9.9	8.0	2.9	(-)	180	1.0	(-)	47	0.0	(-)	0
Y-c int bn	2.1	1.7	1.2	(o)	76	0.0	(o)	0	0.0	(o)	0
Con mod bn	3.7	3.0	1.1	(o)	71	2.4	(o)	110	0.0	(o)	0
Con lt bn	5.6	4.5	9.2	(o)	575	11.2	(+)	503	0.4	(-)	12
Subtotal		80.3			6,232			4,510			3,071

both years elk used more vegetation types in proportion to their availability than MD or WTD (Tables 8 and 9). Elk generally selected habitats of south aspect, variable browse abundance and low to moderate overstory canopy cover (Figs. 10 and 11).

Use of Douglas-fir/xeric and Douglas-fir/open types by MD was greater than availability in January and February 1992 and 1993 (Tables 8 and 9). MD use of the subalpine fir type was also greater than availability during January 1992, and February 1992 and 1993. Use of the Douglas-fir/mature type by MD was not significantly different than availability during January 1992 and 1993, but MD used this type greater than availability in February 1992 and 1993 (Tables 8 and 9). MD used ponderosa pine, burned grassland, and cutover conifer/intense burn types consistently less than availability during 1992 and 1993 (Tables 8 and 9). MD used a wider range of vegetation types during January both years than during February both years. MD generally favored habitats composed of southerly exposures (Fig. 10), abundant browse (Fig. 11) and moderately-open overstory canopy cover (Figs. 10 and 11).

WTD used ponderosa pine/mature, Douglas-fir/larch-pole, and Douglas-fir/mature types significantly greater than availability during January and February 1992 and 1993 (Tables 8 and 9). They used the spruce type in proportion to availability in January 1992, but used it greater than

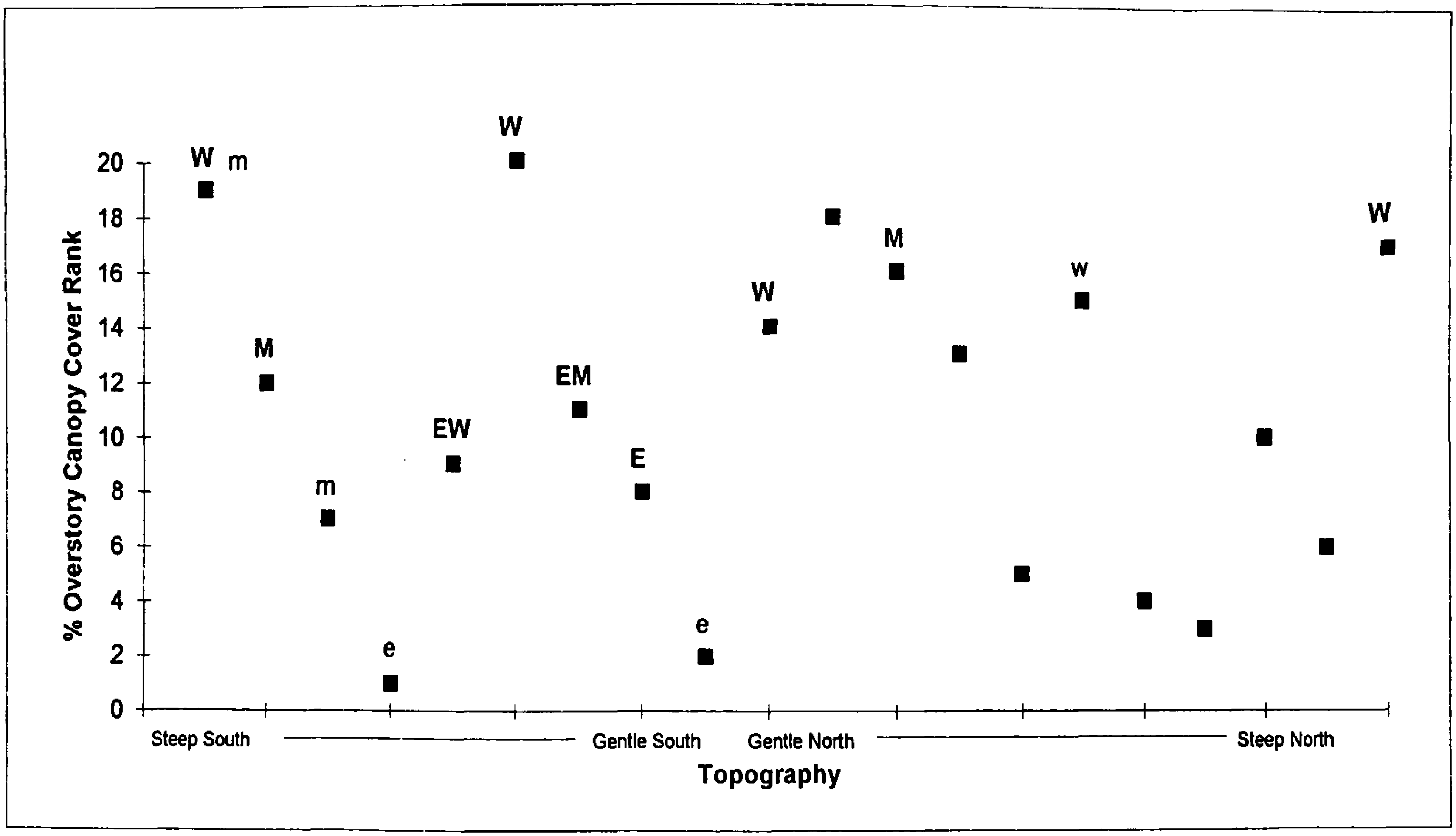


Figure 10. Ordination of 20 vegetation types ranked according to % overstory canopy cover and relative topographic exposure. E,e = elk, W,w = white-tailed deer, M,m = mule deer. Upper-case letters indicate significant use greater than availability (P < 0.10) for 2-4 months during winters 1992 and 1993. Lower-case letters indicate significant use for one month only during winters 1992 and 1993.

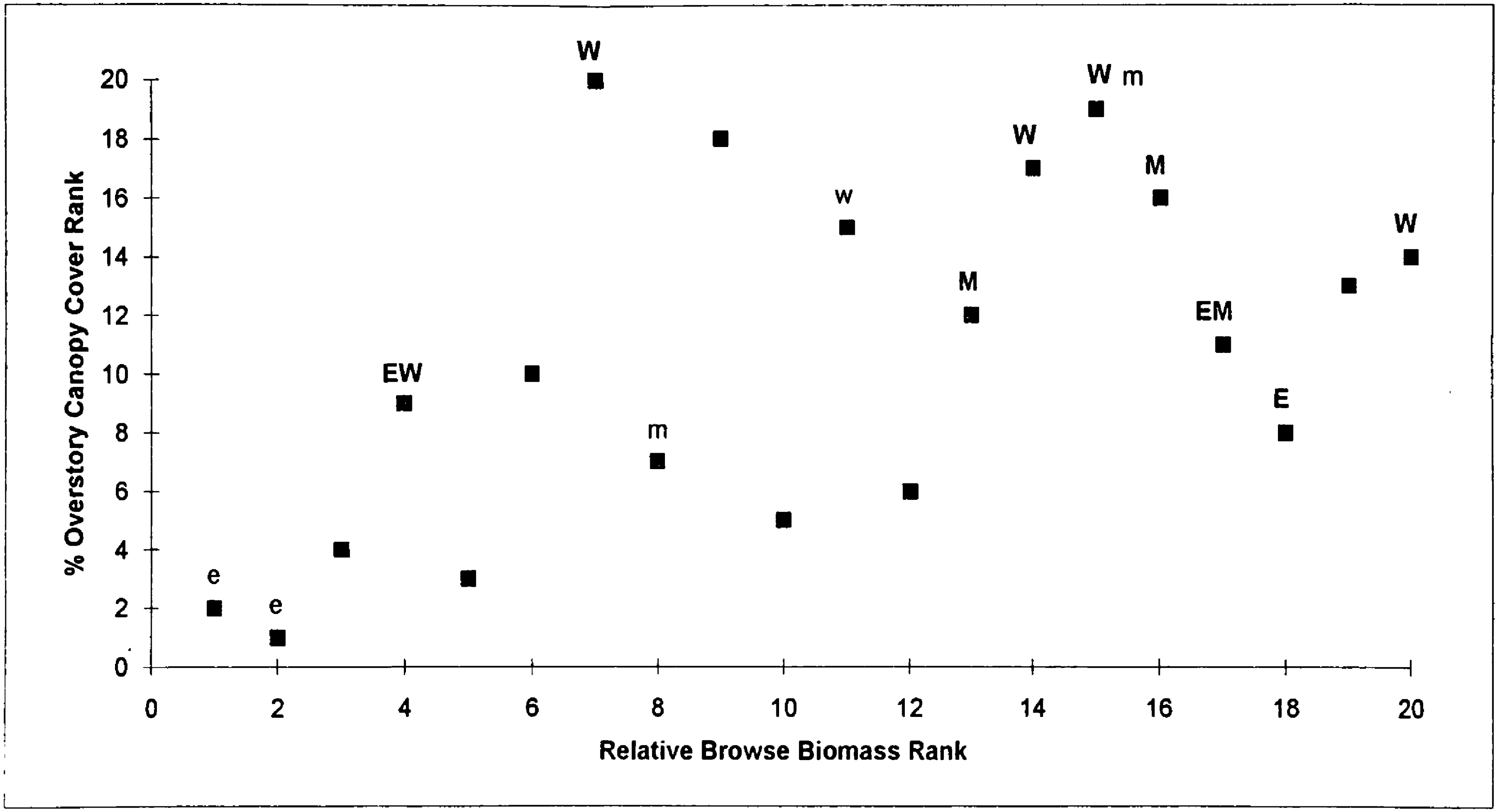


Figure 11. Ordination of 20 vegetation types ranked according to % overstory canopy cover and relative browse biomass. E,e = elk, W,w = white-tailed deer, M,m = mule deer. Upper-case letters indicate significant use greater than availability ($P < 0.10$) for 2-4 months during winters 1992 and 1993. Lower-case letters indicate significant use for one month only during winters 1992 and 1993.

availability in February 1992, and January-February 1993 (Tables 8 and 9). WTD used the ponderosa pine type significantly greater than availability in 1992, but not in 1993. Use of the Douglas-fir/cold type by WTD was greater than availability for both months in 1993, and use of the Douglas-fir/open (cool) type was greater than availability in January 1993 (Table 9). Burned grassland and cutover conifer/intense burn types were used significantly less than availability during January and February 1992 and 1993 (Tables 8 and 9). The conifer/light burn type was used less than availability by WTD in January 1992, but use was not significantly different than availability in January 1993 (Tables 8 and 9). The number of habitats used by WTD, not significantly different than availability remained relatively constant during January and February 1992 and 1993. Overall, high overstory canopy cover appeared to be more important to WTD than browse complexity or slope and aspect; however, southerly aspects received substantial use (Figs. 10 and 11).

Although WTD use of the subalpine fir and young conifer/intense burn types did not significantly differ from availability, no WTD tracks were observed in these types during 1992 or 1993 (Tables 8 and 9). Habitat use less than availability could not generally be evaluated for habitats that comprised less than 4% of the total survey distance.

Four spatial zones were delineated based on cervid distributions documented during the winters of 1991-1993 (Fig. 12). Zone 1 was defined as the area with the greatest number of WTD observations; zone 2 was comprised of core rangelands where elk were commonly observed; zone 3 was the remaining primary winter range where MD were common; and zone 4 was defined as an area that maintained relatively low densities of elk, MD and WTD (Fig. 12).

Elk used spatial zones in proportion to their availability more than either MD or WTD during both winters (Table 10). Also, except for WTD in March 1992, elk tended to use larger areas (Fig. 13). During 1992, elk used zone 2 in proportion to availability, but use was significantly greater than availability in 1993 (Table 10). Elk use of zone 4 was not different than availability in 1992, but use of this area was significantly less than availability in 1993. MD used zone 3 consistently greater than availability, zones 1 and 2 less than availability, and zone 4 not significantly different from availability during both winters (Table 10). WTD showed a strong affinity for spatial zone 1, but consistently avoided zones 2 and 3. WTD generally used zone 4 not significantly different from availability, but used it less during February 1992 (Table 10). Both deer species (with the exception of WTD in March 1992) used relatively small areas (<30 ha) during both winters (Fig. 13). Large areas used by WTD in March 1992 (Fig. 13) resulted because 3 individuals migrated early to

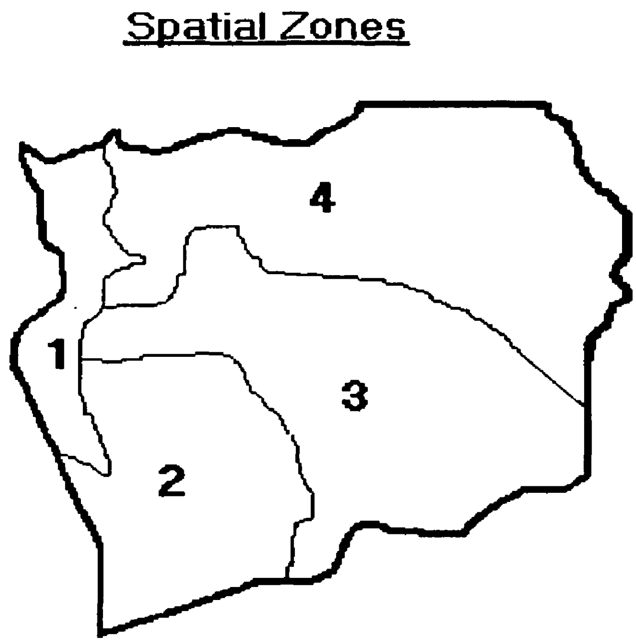


Figure 12. Diagram of spatial zones based on elk, mule deer and white-tailed deer distributions during the winters of 1991-1993.

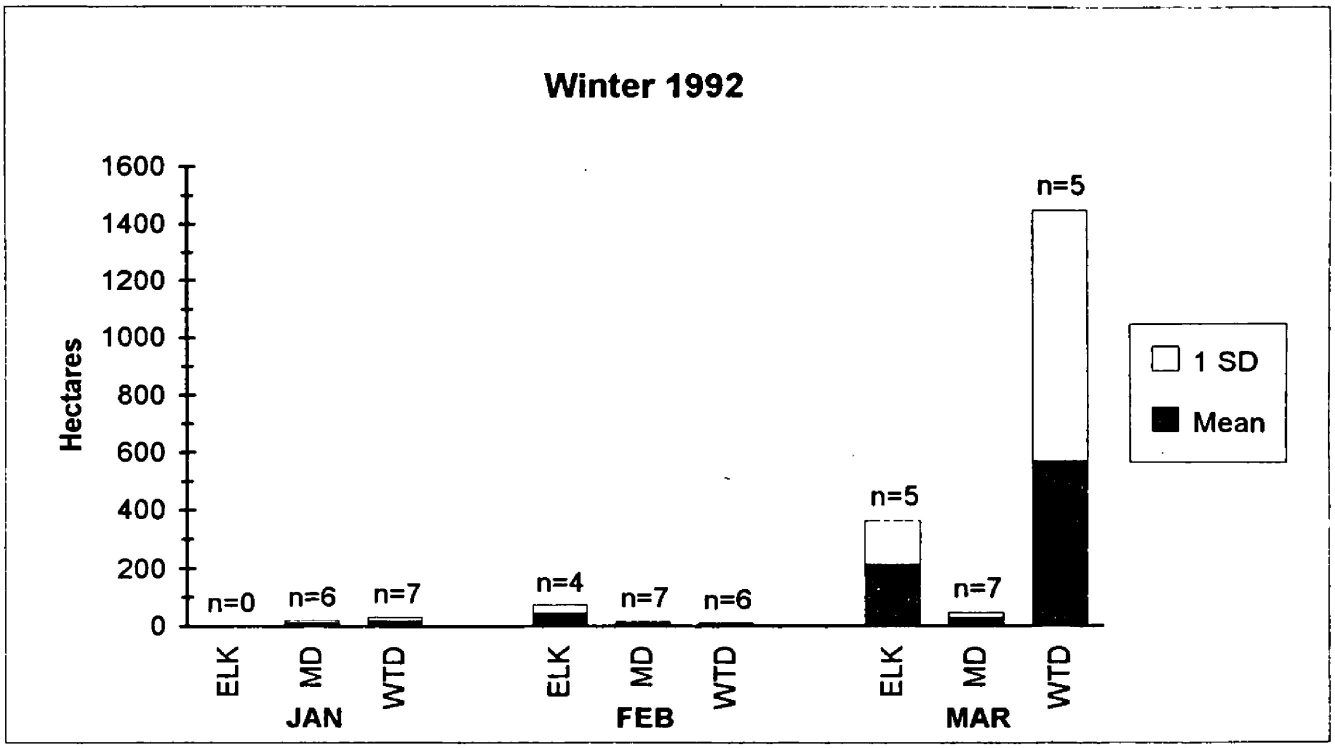
Table 10. Monthly cervid track counts (tks) compared to survey distance (Dis) in 4 spatial zones (Space) on the BCWMA during 1992 and 1993. Use-availability (ua) symbols indicate use significantly greater than availability (+), use significantly less than availability (-) and use not significantly different (o) based on Bonferroni confidence intervals (P < 0.05, Marcum and Loftsgaarden 1980).

January 1992 Space	%Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
1	16.2	13.1	20.0	(o)	1,038	1.0	(-)	85	78.0	(+)	4,245
2	20.7	16.7	21.2	(o)	1,101	2.0	(-)	163	1.8	(-)	95
3	42.1	34.0	42.6	(o)	2,216	75.1	(+)	6,216	0.9	(-)	46
4	21.0	17.0	16.2	(o)	843	21.9	(o)	1,812	19.0	(o)	1,029
Subtotal		80.8			5,198			8,276			5,416

February 1992 Space	%Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
1	15.2	11.0	24.1	(+)	973	7.2	(-)	367	82.9	(+)	2,908
2	22.1	16.0	24.8	(o)	1,000	3.6	(-)	183	1.9	(-)	66
3	40.4	29.2	34.3	(o)	1,381	70.5	(+)	3,605	3.4	(-)	121
4	22.3	16.1	16.8	(o)	678	18.8	(o)	963	11.8	(-)	416
Subtotal		72.2			4,032			5,117			3,510

January 1993 Space	%Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
1	16.3	13.2	11.3	(o)	767	2.0	(-)	148	71.5	(+)	2,675
2	20.6	16.7	37.7	(+)	2,567	1.6	(-)	95	0.9	(-)	35
3	42.2	34.2	38.9	(o)	2,648	75.8	(+)	4,367	8.4	(-)	314
4	20.9	17.0	12.1	(-)	824	20.0	(o)	1,149	19.2	(o)	720
Subtotal		81.1			6,806			5,759			3,744

February 1993 Space	%Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
1	16.3	13.1	10.4	(o)	649	1.1	(-)	48	78.0	(+)	2,414
2	20.6	16.5	42.9	(+)	2,675	0.7	(-)	30	0.6	(-)	19
3	42.0	33.7	34.3	(o)	2,138	78.2	(+)	3,525	1.1	(-)	34
4	21.1	16.9	12.4	(-)	770	20.1	(o)	907	19.7	(o)	604
Subtotal		80.3			6,232			4,510			3,071



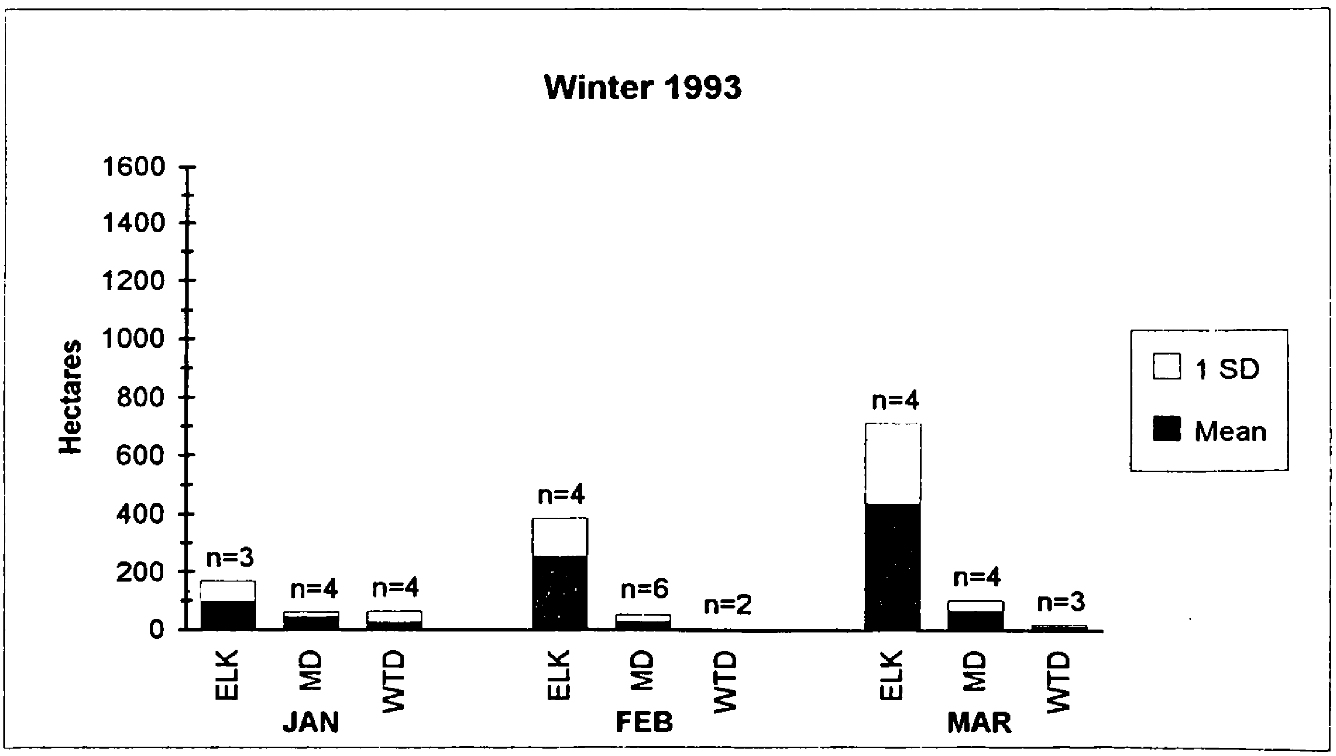


Figure 13. Mean minimum convex polygon areas and standard deviations (1 SD) for radioed cervids on the BCWMA during the winters of 1992 and 1993.

summer range.

Resource Use Overlap

Dietary overlap between elk-MD and elk-WTD species pairs varied between years (Table 11). Variability in monthly dietary overlap was most pronounced during 1993. MD and WTD had the highest dietary overlap of all species pairs for January and February 1992 and 1993, whereas elk and MD had the lowest (Table 11). January and February 1992 overlap indices remained relatively constant for all species pairs. Dietary overlap between elk and both deer species increased from January to February 1993, while overlap between MD and WTD decreased slightly (Table 11).

Habitat overlap indices for all species pairs varied between months and years (Table 11). Overlap between MD and WTD was greater during January than during February of both years. Habitat overlap among cervids tended to be higher in 1992, and the greatest overlap occurred between elk and MD in January 1992. Elk and WTD had the lowest habitat overlap during January and February 1993 (Table 11). Vegetation types ranked by % overstory canopy cover, slope-aspect and relative browse biomass revealed that MD used habitats intermediate to those used by elk and WTD (Figs. 10 and 11).

Spatial overlap indices for the species pairs exhibited consistent patterns (Table 11). Monthly spatial overlap was greatest between elk and MD during both winters, while

Table 11 . Indices of resource-use overlap (Horn 1966) between cervid species on the BCWMA, during winters 1992-93.

Species pair	Diet overlap	Habitat overlap	Spatial overlap	Trophic overlap (DxH)	Ecological overlap (DxHxS)	Cummulative overlap	
	Jan-92	Jan-92	Jan-92	Jan-92	Jan-92	Jan + Feb 1992	
Elk x MD	0.32	0.81	0.80	0.26	0.21	MD & WTD on Elk	0.58
Elk x WTD	0.40	0.63	0.42	0.25	0.11	Elk & WTD on MD	0.51
MD x WTD	0.94	0.73	0.09	0.68	0.06	Elk & MD on WTD	0.35
Sum	1.66	2.17	1.31	1.19	0.38		
	Feb-92	Feb-92	Feb-92	Feb-92	Feb-92		
Elk x MD	0.32	0.67	0.75	0.21	0.16		
Elk x WTD	0.32	0.66	0.49	0.21	0.10		
MD x WTD	0.94	0.49	0.17	0.46	0.08		
Sum	1.58	1.82	1.41	0.88	0.34		
	Jan-93	Jan-93	Jan-93	Jan-93	Jan-93	Jan + Feb 1993	
Elk x MD	0.14	0.49	0.66	0.07	0.05	MD & WTD on Elk	0.18
Elk x WTD	0.24	0.34	0.17	0.08	0.01	Elk & WTD on MD	0.31
MD x WTD	0.93	0.68	0.19	0.63	0.12	Elk & MD on WTD	0.19
Sum	1.31	1.51	1.02	0.78	0.18		
	Feb-93	Feb-93	Feb-93	Feb-93	Feb-93		
Elk x MD	0.29	0.59	0.60	0.17	0.10		
Elk x WTD	0.31	0.34	0.24	0.10	0.02		
MD x WTD	0.85	0.59	0.09	0.50	0.04		
Sum	1.45	1.52	0.93	0.77	0.16		

overlap between WTD and MD was low (Table 11). Elk-WTD spatial overlap was generally intermediate to spatial overlap between elk-MD and MD-WTD pairs. Radio-telemetry data combined for January and February 1992 and 1993 (Fig. 14) supported spatial separation patterns indicated by overlap indices.

Trophic overlap was considered the product of dietary and habitat overlap (May 1975). Trophic overlap was low between elk-MD and elk-WTD pairs, but was consistently high for the MD-WTD pair (Table 11). Trophic overlap for all cervid pairs was lower in January 1993 than in January 1992. Elk trophic overlap with MD and WTD was lower in 1993 than in 1992, and trophic overlap between MD and WTD was greater in January than in February for both years (Table 11). Elk-WTD trophic overlap was generally the lowest of the species pairs during both years.

Ecological overlap was considered the product of dietary, habitat and spatial overlap (May 1975). Ecological overlap was relatively low for all cervid pairs during both years (Table 11). However, ecological overlap was generally higher for species pairs in 1992 than 1993. Elk and MD generally exhibited the greatest ecological overlap (Table 11). The MD and WTD ecological overlap index was greatest in January 1993, and lowest in February 1993 (Table 11). Ecological overlap between elk and MD was greater in January 1992 than in February 1992, but was greater in February than

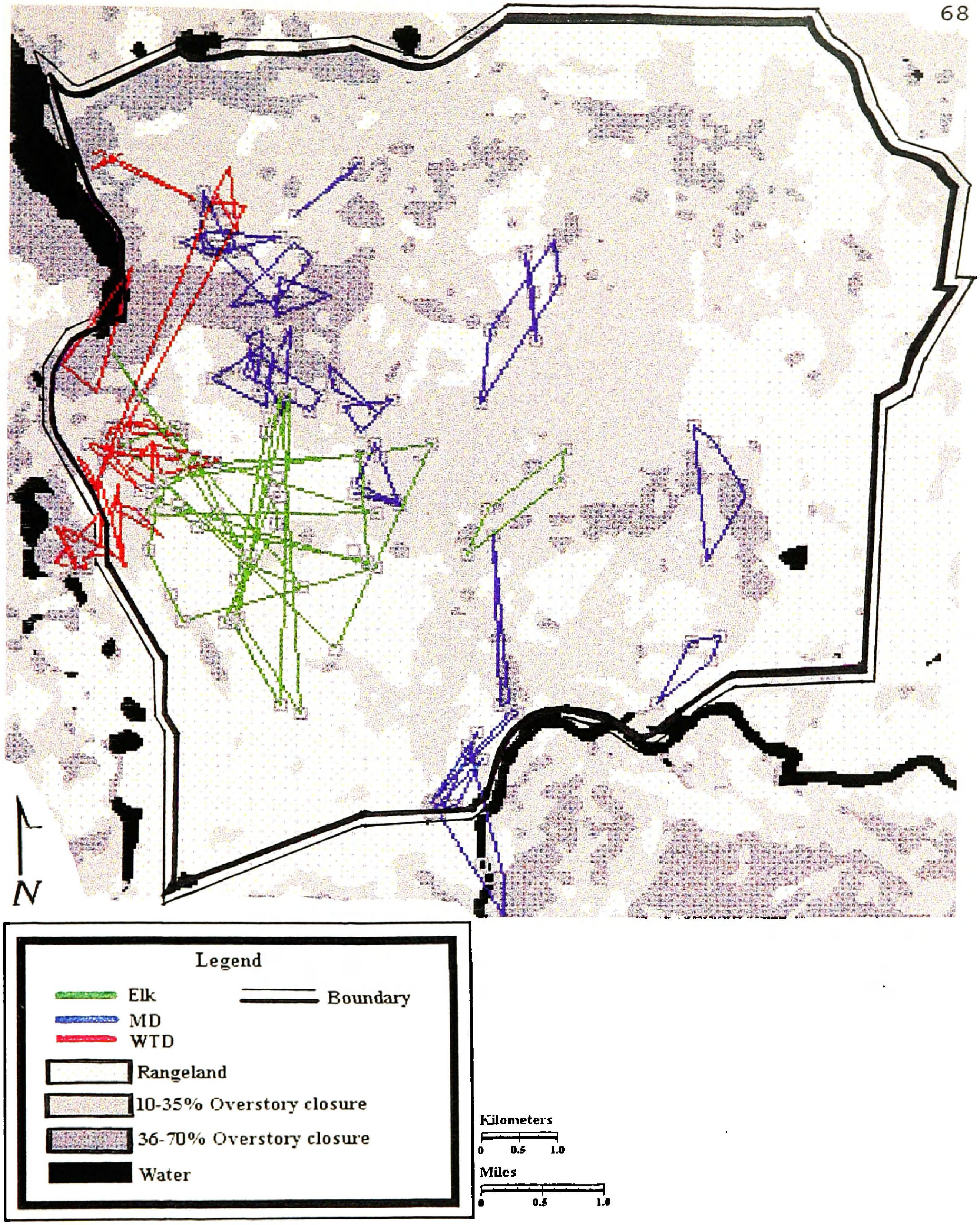


Figure 14. Monthly minimum convex polygons for 5 elk, 8 mule deer and 8 white-tailed deer in January and February 1992 and 1993 on the Blackfoot-Clearwater Wildlife Management Area.

January in 1993. Elk-WTD ecological overlap was intermediate in 1992, but was lowest of all species pairs in 1993 (Table 11). February 1993 had the lowest spatial, trophic and ecological species pair sums of all months examined (Table 11).

Cumulative overlap influence indices were higher in 1992 than in 1993 (Table 11). Cumulative indices indicated that the overlap of MD and WTD resource-use on elk was greatest in 1992. However, the overlap of elk and WTD on MD was also high (Table 11). In 1993, the cumulative influence of elk and WTD on MD was greater than combined species influences on elk or WTD (Table 11).

Winter Weather Conditions

Topography and overstory canopy cover varied among the 20 snow measurement locations sampled during January and February 1992 and 1993. Ranges of measured variables were: slope 0-45%, aspect 5-335°, elevation 1,268-1,646 m, and overstory canopy cover 0-55%. Specific site descriptions are given in Table 12. Coordinates (UTMs) for snow measurement locations are given in Appendix E.

Mobility resistance estimates indicated that snow was more dense and crusted on all sites in 1992 (Fig. 15), but was consistently deeper in 1993 (Fig. 16). All 20 sites had mobility resistance estimates greater than 9.0 in 1992, but sites sm-1 and sl-5 had mobility resistance estimates of 0.0

Table 12. Site characteristics of snow measurement locations monitored on the BCWMA during the winters of 1992 and 1993.

Site[a]	% Slope	Aspect	Elevation (m)	% Overstory canopy
Low elevations				
sl-1	24	180	1,292	2
sl-2 A	0	225p	1,268	0
sl-3	10	290	1,305	0
sl-4 B	8	230	1,268	45
sl-5	5	50	1,353	25
Moderate elevations				
sm-1 C	40	180	1,426	3
sm-2	10	215	1,451	2
sm-3 D	5	270	1,402	35
sm-4	25	90	1,475	10
sm-5	40	50	1,402	5
High elevations				
sh-1	25	280	1,500	0
sh-2	20	205	1,536	15
sh-3 F	15	330	1,548	55
sh-4	20	190	1,646	30
sh-5	30	200	1,622	2
Northerly aspects				
sn-1	45	320	1,463	35
sn-2	10	5	1,536	20
sn-3 E	20	330	1,609	5
sn-4	15	20	1,445	20
sn-5	30	335	1,451	35

a = Upper case letters indicate that mean temperatures, snow severity and winter severity indices were calculated for these sites.
p = Prevailing aspect.

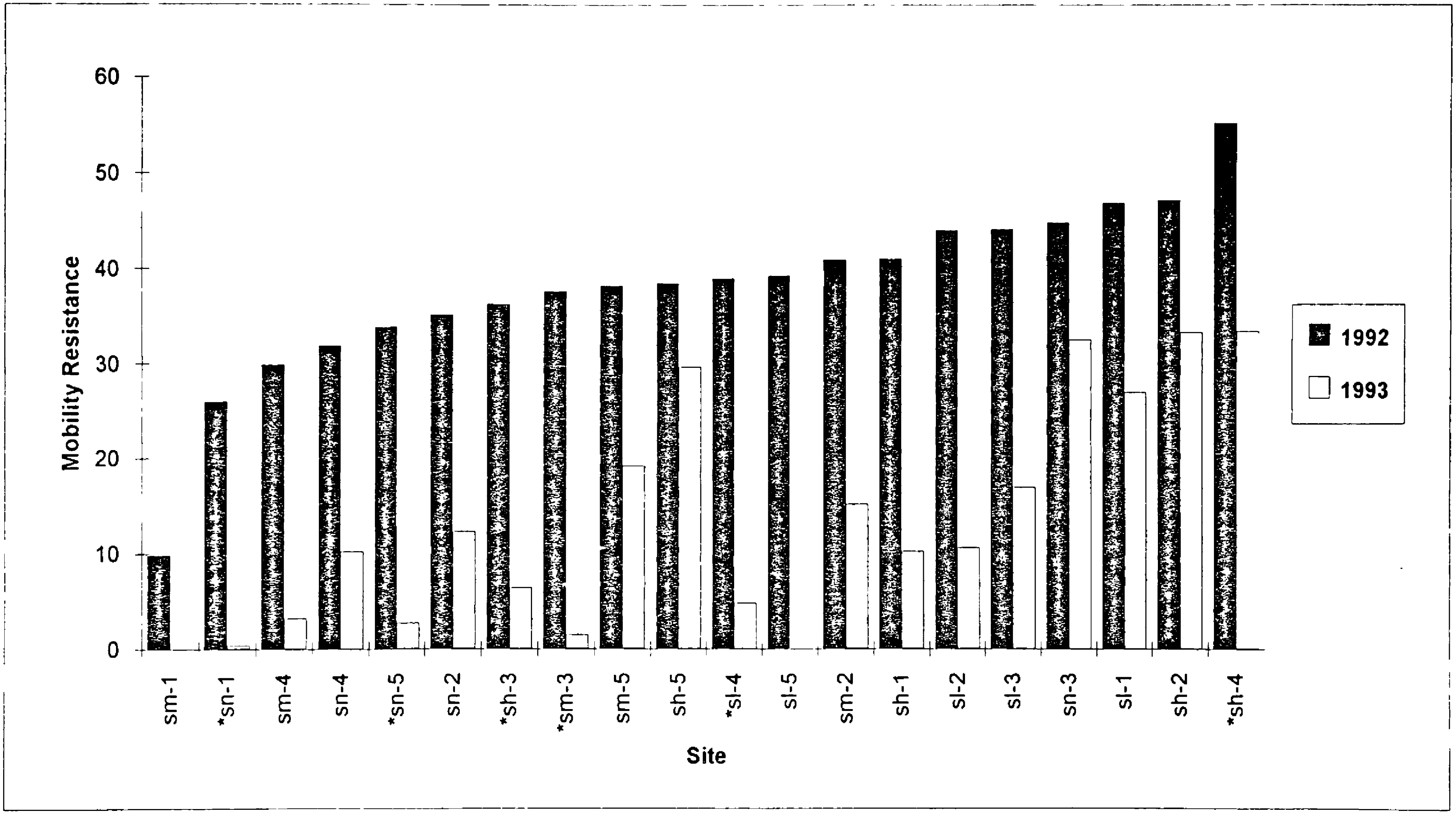


Figure 15. Snow mobility resistance indices (MR) for 20 sites monitored on the BCWMA during January and February 1992 and 1993.

* Sites with >29% overstory canopy cover.

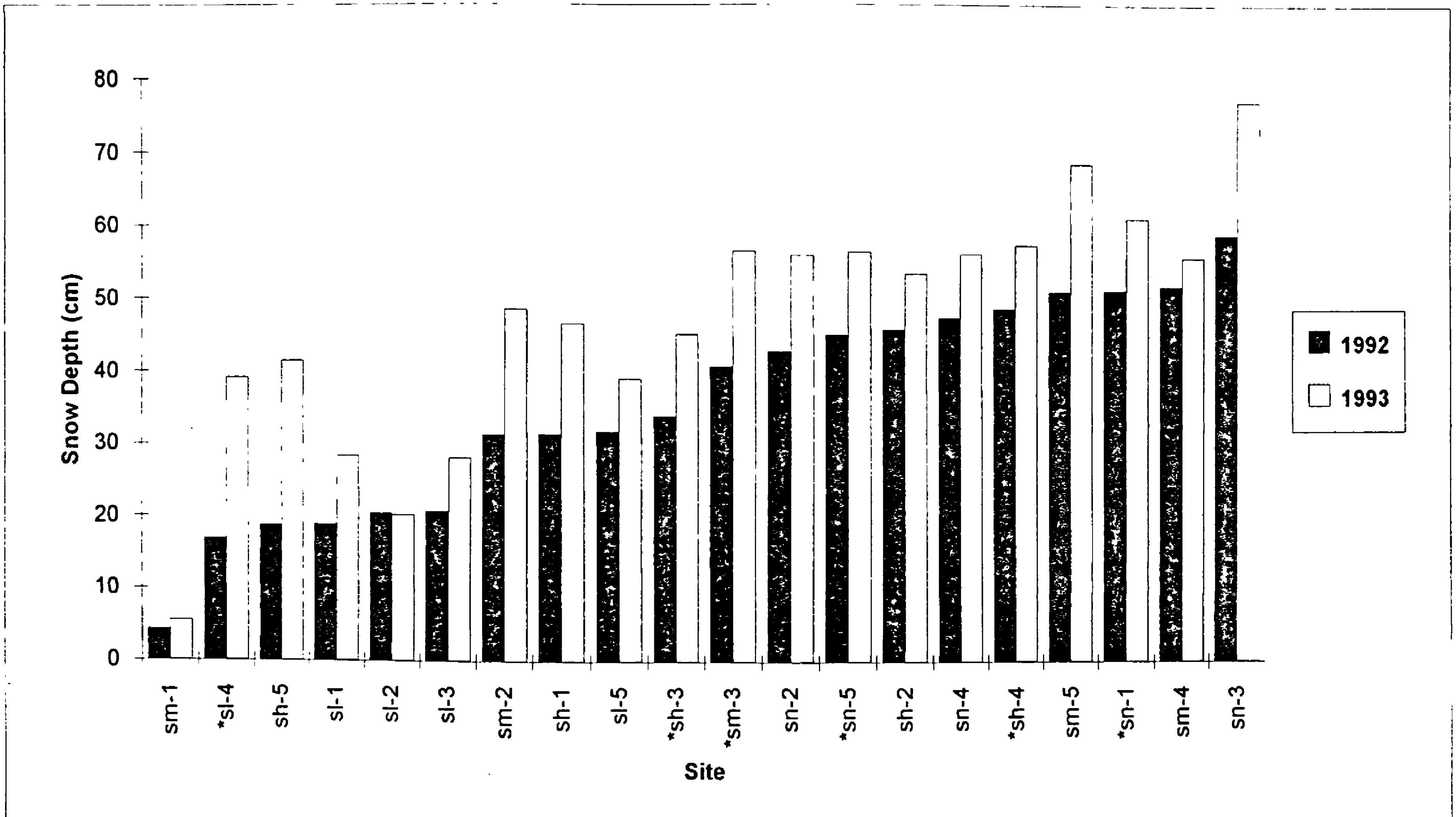


Figure 16. Mean snow depths (Depth) for 20 sites monitored on the BCWMA during January and February 1992 and 1993.

* Sites with >29% overstory canopy cover.

in 1993 (Fig. 15). The lowest mobility resistance and snow depth estimates for both years were observed on site sm-1, which was a steep, exposed site of moderate elevation and south exposure (Table 12). The highest mobility resistance estimates were observed for sh-4, and sn-3 had the greatest snow depth estimates for both years (Figs. 15 and 16). Both sn-3 and sh-4 were high elevation sites (>1,600 m) with gentle slopes and substantial exposure to solar radiation. Exposure to solar radiation on sn-3 was likely influenced by its gentle northerly slope and sparse canopy closure, whereas exposure on sh-4 was influenced more by southerly aspect (Table 12). Sites ranked according to mobility resistance and snow depth in 1992 did not maintain their ranks in 1993 (Figs. 15 and 16).

Snow severity indices calculated from combined mobility resistance and snow depth data indicated that the total influence of snow was less in 1993, although snow depths were greater (Fig. 17). Snow severity was lowest at site sm-1, and was greatest for sites sn-3 and sh-4.

Overstory canopy cover did not appear to influence snow severity in 1992. However, sites with overstory canopy cover >29% generally had lower snow severity estimates in 1993 (Fig. 17). Sites ranked according to snow severity in 1992 did not maintain their ranks in 1993 (Fig. 17).

Maximum temperatures for snow measurement locations established at the lowest elevations tended to be greater

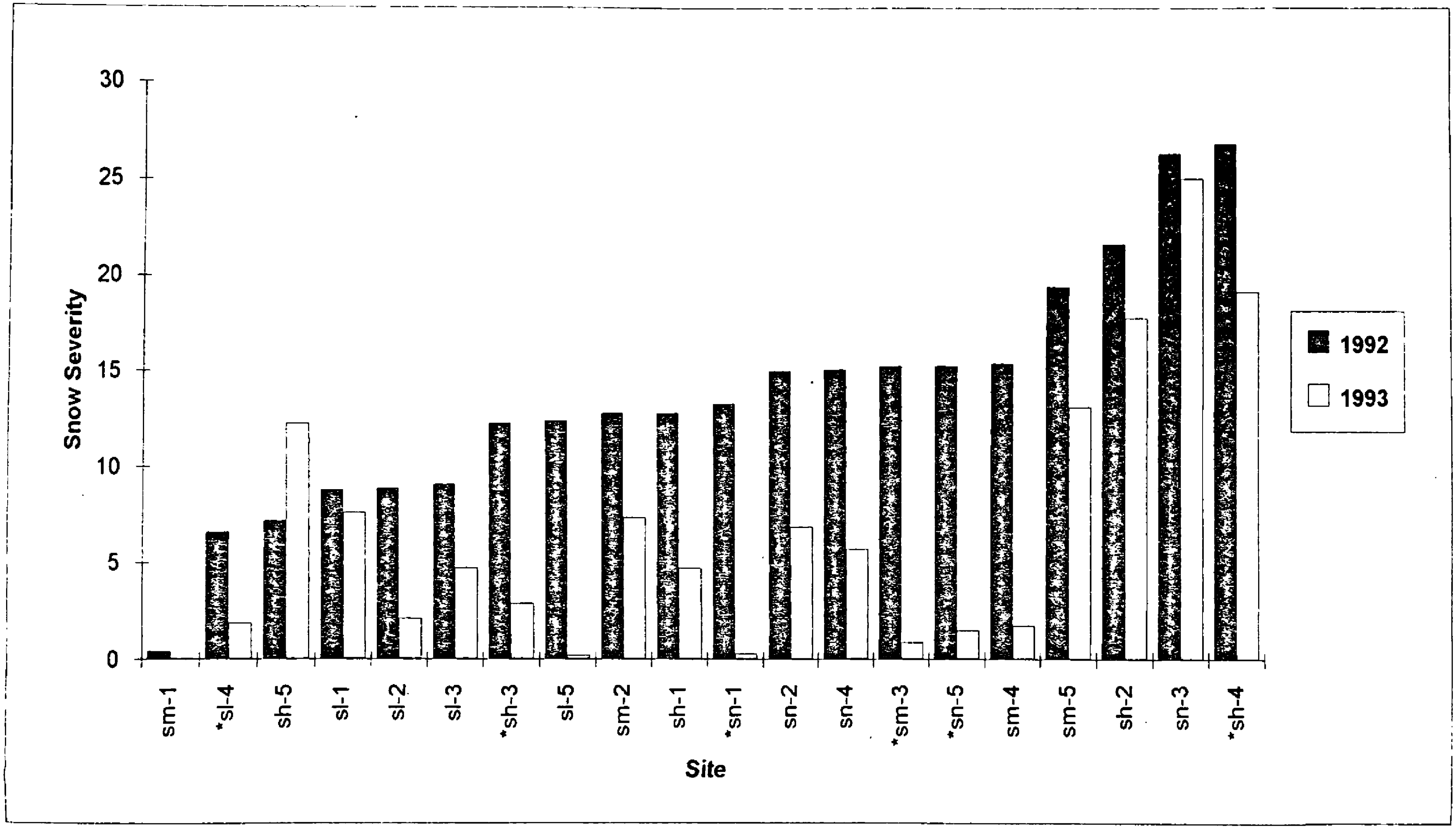


Figure 17. Snow severity indices (SS) calculated from combined mobility resistance and snow depths for 20 sites on the BCWMA during January and February 1992 and 1993.

* Sites with >29% overstory canopy cover.

than for other sites (sites A and B, Table 13). However, the mildest minimum temperatures both winters were recorded for site F, which occurred on a high elevation northerly exposure (Table 13). Site F had the greatest overstory canopy cover observed (55%) for all temperature locations (Table 12). Site E also occurred on a high elevation northerly exposure (Table 12); however, maximum and minimum temperatures there were lowest during both winters (Table 13). Overstory canopy cover at site E was only 5% (Table 12). Site B had substantial overstory canopy cover (45%), and maximum temperatures recorded there in 1993 were considerably higher than for other sites that winter (Table 13).

Winter severity indices that combined snow and temperature variables for sites A-E (Table 12) indicated that winter 1993 was harsher than winter 1992 (Table 13). The index developed for the BCWMA and the index of Picton and Knight (1970) varied considerably by site and by year. Picton and Knight's (1970) index was derived from temperature and snow depth data, and did not consider snow crust and density characteristics throughout winter. Both indexes gave similar results in 1992. However, Picton and Knight's (1970) index gave a higher estimate for sites B and D, and lower estimates for A, C, and E in 1993 when compared with the index that incorporated snow mobility resistance (Table 13). Site rankings based on winter severity were

Table 13. Mean maximum/minimum temperatures (Max/Min), snow severity indices (SS), and winter severity indices (WS) for 6 stations monitored weekly during January, February and March 1992 and 1993 on the BCWMA.

	Max/Min ($\bar{x}$° C)		SS[a]		WS			
					Baty[b]		Picton[c]	
Site	1992	1993	1992	1993	1992	1993	1992	1993
A	14/-11	7/-21	8.9	2.1	3.4	19.6	1.0	13.5
B	12/-12	11/-18	6.6	1.9	5.2	9.9	4.2	14.7
C	8/-9	6/-18	0.4	T[d]	1.0	14.8	6.4	10.5
D	9/-12	7/-20	15.3	0.9	17.9	16.3	18.0	27.8
E	7/-11	2/-22	26.3	25.0	30.3	49.9	29.6	44.8
F	/-7	/-15	12.3	2.9				

[a] (100 - % $\bar{x}$ sinking depth) · ($\bar{x}$ snow depth)/100 = SS.
[b] (($\bar{x}$ °C) · -2.7) + SS - 1.425 = WS. Scaled with 1.0 as the lowest value.
[c] Adapted from Picton and Knight (1970). Scaled with 1.0 as the lowest value.
[d] T = trace (<0.1).

also not consistent between years (Table 13).

Use-availability results for 4 snow depth classes revealed that elk used more classes not significantly different from availability than MD or WTD (Table 14). WTD used the deepest snow classes less than availability, while MD used them greater than or not significantly different than availability (Table 14). MD tracks were more abundant in the 21-40 cm and 41-60 cm snow depth classes, whereas WTD tracks were more abundant in the 0-20 cm and 21-40 cm classes. In February 1993 elk and WTD used classes <61 cm not significantly different from availability. MD used the 0-20 cm class greater than availability in February 1993; however, sites with such little snow were rare (Table 14). Mean snow depths in the 61+ cm and 0-20 cm classes were not observed for any transect segment in February 1992 and January 1993 respectively (Table 14).

The 2 most severe mobility resistance classes for January 1993 were not observed, which indicated that snow imposed less resistance on cervids in January than in February (Table 15). Elk and MD consistently used all mobility resistance classes not significantly different from availability, whereas WTD used areas with lowest mobility resistance greater than availability (Table 15). Qualitative climatic descriptions for 1992 and 1993 are provided in Table 16.

Table 14. Monthly cervid track counts (tks) compared to survey distance (Dis) in 4 snow depth classes (Snow dpth) on the BCWMA during 1992 and 1993. Use-availability (ua) symbols indicate use significantly greater than availability (+), use significantly less than availability (-) and use not significantly different (o) based on Bonferroni confidence intervals ($P < 0.05$, Marcum and Loftsgaarden 1980).

January 1992

Snow dpth cm	%Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
0-20	11.9	9.6	14.9	(o)	774	0.7	(-)	62	33.3	(+)	1,805
21-40	69.4	56.1	71.4	(o)	3,712	79.8	(+)	6,607	63.0	(o)	3,410
41-60	17.5	14.1	13.7	(o)	710	19.4	(o)	1,602	3.7	(-)	201
61+	1.2	1.0	0.0	(o)	2	0.1	(o)	5	0.0	(o)	0
Subtotal		80.8			5,198			8,276			5,416

February 1992

Snow dpth cm	%Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
0-20	26.6	19.2	32.0	(o)	1,289	11.2	(-)	573	50.3	(+)	1,764
21-40	63.9	46.1	64.1	(o)	2,585	83.8	(+)	4,287	48.8	(-)	1,714
41-60	9.5	6.9	3.9	(-)	158	5.0	(o)	257	0.9	(-)	32
61+	0.0	0.0									
Subtotal		72.2			4,032			5,117			3,510

January 1993

Snow dpth cm	%Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
0-20	0.0	0.0									
21-40	49.6	40.3	60.4	(+)	4,109	38.7	(-)	2,230	70.2	(+)	2,627
41-60	47.2	38.3	39.4	(o)	2,680	60.4	(+)	3,478	29.8	(-)	1,117
61+	3.2	2.6	0.2	(o)	17	0.9	(o)	51	0.0	(-)	0
Subtotal		81.1			6,806			5,759			3,744

February 1993

Snow dpth cm	%Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
0-20	0.5	0.4	1.0	(o)	63	3.4	(+)	153	0.1	(o)	4
21-40	32.9	26.5	39.5	(o)	2,460	23.7	(-)	1,069	40.2	(o)	1,234
41-60	56.6	45.5	55.5	(o)	3,460	65.4	(o)	2,949	58.2	(o)	1,786
61+	10.0	8.0	4.0	(-)	249	7.5	(o)	339	1.5	(-)	47
Subtotal		80.3			6,232			4,510			3,071

Table 15. Monthly cervid track counts (tks) compared to survey distance (Dis) in 4 snow mobility resistance index classes (MR) on the BCWMA during 1993. Use-availability (ua) symbols indicate use significantly greater than availability (+), use significantly less than availability (-) and use not significantly different (o) based on Bonferroni confidence intervals ($P < 0.05$, Marcum and Loftsgaarden 1980).

January MR	1993 %Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
0-12	95.7	77.7	95.7	(o)	6,513	96.9	(o)	5,579	99.6	(+)	3,731
13-25	4.3	3.5	4.3	(o)	293	3.1	(o)	179	0.4	(-)	14
26-37	0.0	0.0									
*38-50	0.0	0.0									
Subtotal		81.1			6,806			5,759			3,744

February MR	1993 %Dis	Dis km	%Elk	ua	Elk tks	%MD	ua	MD tks	%WTD	ua	WTD tks
0-12	53.9	43.3	58.2	(o)	3,624	58.9	(o)	2,658	70.0	(+)	2,170
13-25	24.5	19.7	22.1	(o)	1,380	23.7	(o)	1,068	9.6	(-)	296
26-37	17.8	14.3	15.5	(o)	966	15.0	(o)	678	19.7	(o)	605
*38-50	3.7	3.0	4.2	(o)	262	2.4	(o)	106	0.0	(-)	0
Subtotal		80.3			6,232			4,510			3,071

* Elk, MD and WTD could occassionally walk on the snow surface at this MR level.

Table 16. Qualitative summary of environmental conditions on the BCWMA during winters 1992 and 1993.

1992	1993
JANUARY	**JANUARY**
Weather/Snow Snow persistent from December, little January snowfall. Moderate temperatures. Snow moderately restrictive.	**Weather/Snow** Deep snow and high wind. Snow powdery and not dense. Cold temperatures early in month but moderated. Warmer temperatures and rain late in month.
Forage Low bunchgrass availability in burn for elk and reduced forage and cover availability for MD along Sperry Grade.	**Forage** Abundant forage in burn. Fair snow-influenced forage availability. Snow relatively deep, but not highly restrictive.
FEBRUARY	**FEBRUARY**
Weather/Snow Occassional rain and refreezing of persistent snow. Snow dense and crusted restricting movement. Trace of additional snowfall. Warm daily temperatures.	**Weather/Snow** Mild early temperatures. Later very cold, high wind, and heavy snow.
Forage Poor bunchgrass forage availability for elk and reduced forage and cover availability for MD along Sperry Grade. South slopes becoming snowfree. Green forage available by February 14. Tree wells snowfree and provided access to forage.	**Forage** Abundant forage in burn. Poor snow-influenced forage availability. Snow deep and restrictive.
MARCH	**MARCH**
Weather/Snow Unseasonably warm. Snow very patchy and less restrictive.	**Weather/Snow** Cold temperatures and wind early, moderated later in the month. Persistent deep dense snow, mushy during the day.
Forage High forage availability in tree wells and on exposed slopes. Abundant green forage in burn and snow-free exposures.	**Forage** Sparse openings on wind swept south exposures. Tree wells snow-free. Availability rapidly increasing. Green forage available by March 15.

DISCUSSION

Population Estimates and Winter Mortality

Cervid density was conservatively estimated at 28/km^2 during this study, which was considerably greater than ungulate densities observed during other similar studies (4.7/km^2, Singer 1979; 19/km^2, Constan 1972; and 9.5/km^2, Mackie 1970). High cervid densities on the study area were expected to increase the potential for resource partitioning in response to interspecific competition (Schoener 1982), or increase resource use overlap, thus intensifying interspecific competition (Jenkins and Wright 1988).

Mortality estimates for the 3 cervid species during both winters were low compared with results of other regional studies (Baremore 1980 as cited by Houston 1982:57, Wood et al. 1989, Pac et al. 1991). However, slight increases in MD and WTD carcasses were observed in 1993. These increases were presumably due to more severe winter conditions, increased mountain lion (*Felis concolor*) predation or chance occurrence. Examinations of femur marrow (Cheatum 1949) indicated that mortality due to malnutrition was of minor importance during both winters.

Only marked elk, MD and WTD were used to estimate hunting mortality during this study. Hunting was the greatest known source of mortality for female elk, which was influenced by 150 and 200 antlerless permits issued for the study area during 1992 and 1993 respectively. Hunting mortality estimates for male elk (>0.5 years of age) that wintered on the study area from 1987-1989 averaged about 47% (Hurley 1994). However, hunting of males was restricted to hunting districts outside district 282. More liberal buck harvest regulations on the study area and surrounding hunting districts influenced greater observed hunting mortality of male deer.

Mortality data supported the conclusion that hunting had substantial potential for limiting the elk population. Results of mortality estimates also indicated that hunting and auto collisions had high potential for controlling MD and WTD populations. Overall, low observed winter mortality indicated that cervid densities had not exceeded ecological carrying capacity (Caughley 1979).

Forage Use

Monthly and yearly variability existed in all cervid diets. Shifts in elk, MD and WTD diets presumably reflected intraspecific forage preferences (Hansen and Clark 1977), and differential forage availabilities in occupied habitats (Jenkins 1985). Forage availability was influenced by the 1991 wildfire, snow conditions and plant phenology.

In contrast with Jenkin's (1985) study, differences in forage availability between months and years on the BCWMA were difficult to distinguish. The October 1991 wildfire completely removed forage (primarily bunchgrass) from about 33% of the study area. However, the winter of 1992 was relatively mild, and green forage was available one month earlier than in 1993. In 1993, an ample standing crop of bunchgrass was present both in and outside the burn, snow was deeper but generally not as dense and crusted, and temperatures were colder. Thus, forage availability in 1992 was limited more by wildfire-caused removal, whereas poor snow conditions limited forage availability more in 1993.

Elk were probably affected more by the burn than deer. A large portion of the wintering elk population dispersed early from the study area in 1992. Elk remaining on the study area increased use of elk sedge and browse found in forested habitats because foraging conditions in burned grasslands were unfavorable. Although elk foraged more in forested habitats in 1992, their use of graminoids remained high and relatively constant during both winters.

Forage use data suggested that MD and WTD were more affected by winter conditions observed in 1993 than by burn effects in 1992. They relied more on conifers than on nutritious species, such as Oregon grape (Jenkins 1985) in February 1993. In March 1992 and 1993, MD and WTD switched from conifers to other forage species, taking immediate advantage of newly available forage items (persistent and new growth).

WTD maintained nearly identical forage class compositions in winter diets (for January-March combined) during both years. This suggested that WTD possessed an ability to acquire preferred forage under varied environmental conditions. This also may have reflected a higher inherent availability of low growing forage species in habitats with greater overstory canopy coverage.

Deciduous shrubs were an integral part of cervid diets. However, based on food habits data and field observations, deciduous browse did not appear to be highly preferred by elk, MD or WTD, and it was used most when other forage types were less available. Percentages of deciduous browse observed in diets may have been somewhat under-represented because of lower inherent ratios of identifiable epidermal fragments (Gill et al. 1983, Holechek and Valdez 1985).

Conifer use by MD and WTD was high in early January of both years, even when deciduous browse was both abundant and available. Conifers were also used substantially by MD and WTD when low-growing forage was more exposed in January 1994. Elk diets also contained conifer (10-22%) during all 4 months examined.

Observations made by Greer et al. (1970) indicated that a high percentage of conifer observed in elk rumen was an indicator of poor nutritional condition. However, the observations of Greer et al. (1970) may also have been influenced by the quality of plant parts ingested (Hobbs et al. 1983:5), conifer use tolerance (Dietz et al. 1962), and influence of seasonal range conditions (Wood et al. 1989:35, Hamlin and Mackie 1989). I agree with Jenkins (1985:74), that conifer should probably be considered a winter dietary staple for elk and deer in western Montana rather than emergency forage.

High use of evergreen shrubs (primarily Oregon grape) by cervids in late winter was likely a result of its high forage value (Jenkins 1985), and increased availability in snow-free tree wells. Quantification of the abundance and use of tree lichens (Alectoria spp.) was beyond the scope of this study, but daily observations of feeding cervids indicated that lichens were favored by all three species.

Six forage species (in addition to tree lichens) were identified as staple winter forage items for cervids on the BCWMA: (1) rough fescue, (2) Douglas-fir, (3) ponderosa pine, (4) Oregon grape, (5) elk sedge, and (6) serviceberry. This rating was based on the frequency and amount of plants consumed by elk, MD and WTD, as influenced by forage availability and animal densities on the study area.

Fecal Analysis

All procedures currently used for estimating the botanical composition of ungulate diets have advantages and disadvantages (Holechek et al. 1982a). There is little agreement in the literature regarding the precision and accuracy of fecal analysis (Holechek et al. 1982a). However, other alternatives present similar or greater problems than fecal analysis. Several studies that tested the reliability of fecal analysis utilized methods for comparison based on unique assumptions, and may be unreliable (Anthony and Smith 1974, Gill et al. 1983) as implied by Lewis (1994) and Holechek et al. (1982a).

Several authors have questioned the accuracy of fecal analysis (Holechek et al. 1982b). Accuracy of the fecal analysis technique could be influenced by: (1) differential digestibility of forage items; (2) variable fragmentation characteristics of forage items; (3) differing identifiable leaf-stem ratios for ingested plant species; (4) general difficulty distinguishing different species; and (5) differences in observers and their experience levels (Dearden et al. 1975; Holechek et al. 1982a,b; Gill et al. 1983; Holechek and Valdez 1985). Other researchers have suggested that fecal analysis is comparable to rumen analysis and is superior in several respects (Anthony and Smith 1974, Lewis 1994).

To compare cervid diets, I assumed that digestibility biases of forage items consumed by elk, MD and WTD were similar in winter. If this assumption was valid, the accuracy of food habits results was of little importance for estimating resource-use overlap. Factors that increased the reliability of fecal analysis estimates for this study were:

(1) pellet group samples represented individual time periods and were collected in greater quantities than the minimum number of 15 suggested by Anthony and Smith (1974), (2) composites were analyzed with 200 microscope fields to reduce variability and improve accuracy, (3) effects of differential digestibility should have been less for cured winter vegetation samples (Vavra et al. 1978), and (4) individual forage species observed in elk, MD and WTD diets were from one study area and should have exhibited similar fragmentation traits.

Habitat and Spatial Use

Variability in habitat selection by cervids was probably in response to forage availability (Jenkins and Wright 1988), energetic costs of movement relative to snow depth (Parker et al. 1984) and snow crust in different habitats (Verme 1968), and thermal differences between habitats (Moen 1976).

In 1992, elk were unable to graze on bunchgrass in preferred grasslands as a result of the 1991 burn; thus, they spent more time in forested habitats. In January 1993, elk used grasslands that burned in fall 1991 extensively, but made greater use of forested browse types and adjacent unburned grasslands in February 1993. Substantial use of open Douglas-fir and adjacent unburned grassland habitats when snow was deep in February 1993 indicated that foraging conditions in burned grasslands had deteriorated. Elk typically used habitats with lower percentages of overstory canopy cover and greater amounts of fibrous forage than MD or WTD. This suggested that elk were less restricted by snow, cold temperatures and forage quality.

MD consistently used Douglas-fir habitats with relatively sparse overstory canopy cover (means <30%), but shifted use to mature Douglas-fir stands with higher overstory canopy cover ($\bar{x}$ = 53%) as snow increased in depth and crust. MD also used high elevation ($\bar{x}$ = 1,570 m) subalpine fir habitat with a mean overstory canopy cover of 48% during February of both years. Although snow was deep in subalpine fir habitat, its north exposure and relatively dense overstory canopy mitigated adverse snow depth and crust conditions. Subalpine fir habitats were close to mature Douglas-fir stands, which may have influenced observed use of subalpine fir types by MD. The lower number of vegetation types used in February both years indicated that MD movement was more restricted in mid-winter. Reduced movement probably resulted from lowered metabolism in winter (Moen 1978), increasingly dense and crusted snow (Verme 1968), and decreased mid-winter physical condition.

Habitats used by WTD generally had shallower snow, less crusted snow, and higher daily temperatures than other habitats on the study area. WTD generally used relatively level habitats with abundant overstory canopy cover (41-

53%), and variable shrub understories. Habitats used most by WTD were predominantly on southwest and west exposures. They also made substantial use of adjacent non-forested foraging areas (southwest exposures with slopes of 50-90%), and north aspect pole stands. Steep non-forested sites offered browse, forbs, early green vegetation, and low snow accumulations. North aspect pole stands contained substantial amounts of tree lichen, and moderately deep but less crusted snow.

The number of habitats used by WTD remained relatively constant during both winters, which suggested minimal habitat shifting. Observations made incidental to capturing cervids in 1991, suggested that WTD shifted from habitats with sparse overstory canopy (<30%) to denser overstory canopy (>50%) as snow depth increased in late December or early January. Small areas were used by radio-collared WTD in January and February 1992 and 1993, which suggested that their movements were restricted by snow. Minimal observed WTD movement was also probably influenced by lowered metabolic rate in winter (Moen 1978) deep crusted snow (Verme 1968), and decreased mid-winter physical condition.

Elk used larger areas on the BCWMA which suggested that they were less restricted by snow than MD or WTD. Use of relatively small areas and selection of the lowest now depth class by elk in January 1993 probably reflected a preference by elk for bunchgrass forage in areas with shallow snow, rather than snow conditions that restricted movement. Spatial zone 2 was comprised of burned and unburned grassland habitats that likely received increased elk use in 1993 as a result of greater forage abundance. Elk use of zone 4 in 1992 and avoidance of zone 4 in 1993 implied that elk dispersed, and used less preferred forested habitats in 1992 as a result of the fall 1991 wildfire.

Use of spatial zones by MD and WTD changed little during both years. Zone 3 was favored by MD in January and February during both years. Radio locations of collared MD also supported individual affinities for spatial zone 3. WTD favored zone 1 where snow was shallowest and least crusted. Radio-collared WTD also maintained affinities for spatial zone 1. The avoidance of zone 4 (primarily composed of north aspects) by WTD in February 1992 was probably in response to early green-up, snow-free conditions on adjacent south slopes, and early dispersal from primary winter habitats. Overall, WTD had smaller herd home ranges than MD or elk during both winters.

Resource Use Overlap

Resource use overlap indices indicated that overlap between species pairs varied temporally with changes in environmental conditions, and subsequent forage availability. Overlap indices suggested that mechanisms for substantial resource partitioning existed which potentially mitigated interspecific competition among elk, MD and WTD. Although MD and WTD exhibited the greatest dietary overlap, they generally maintained the lowest spatial overlap, which resulted in low ecological overlap. Although elk and MD consistently exhibited the greatest spatial overlap, they maintained the lowest dietary overlap. Ecological overlap between elk and both deer species was mitigated by the preference by elk for graminoids, and by their broader use of habitats and space. Increased dietary, habitat and spatial overlap between elk-MD and elk-WTD in 1992 implied that the removal of substantial amounts of bunchgrass forage by the 1991 wildfire resulted in greater ecological overlap during 1992 than the relatively severe winter conditions observed in 1993.

Movement and forage availability were most limited by snow and cold temperatures during February 1993. However, spatial, trophic and ecological overlap sums were the lowest observed. This implied that the combined influences of ecological overlap and potential competitive interactions among elk, MD and WTD were lowest during the period when observed winter weather conditions were most severe, or that competition was severe enough to cause a strong partitioning response.

Ecological overlap between the species of similar body size (MD and WTD) was also consistently low for the months with the deepest and/or most crusted snow. Overlap between the species with the greatest difference in body size (elk and WTD) was only slightly lower when snow was deepest in February 1993. Ecological overlap indices suggested that competition was most likely between elk and MD during periods with low forage availability. Furthermore, MD appeared more likely to suffer from competition as a result of the combined influences of elk and WTD in winter.

Although MD and WTD maintained relatively high trophic overlap, they were spatially separated. Habitats with similar structure and plant species were used by MD and WTD, but not in the same spatial subunits. This observation suggested that use of habitats and space by one deer species was being restricted by the other. Interspecific aggressive behavior among MD and WTD was never observed, but intraspecific aggression was frequently observed for both species. Possibly, non-aggressive disturbance occurred between MD and WTD. According to Deniston (1956), disturbance occurs where two or more species occupy the same range and one species leaves the vicinity of another. The species that leaves the area may simply be intimidated or annoyed by the mere presence of the other species (Nelson 1984).

Although detailed investigation of the mechanisms for such interactions between MD and WTD was beyond the scope of this study, high observed WTD densities in some areas were probably a factor in this relationship. Most WTD migrated abruptly to the west portion of the study area (spatial zone 1) in December or early January as snow depth increased. MD were less likely to seek habitats with shallow snow early, which allowed WTD to passively fill preferred winter habitats that existed in the western subunit. MD were more frequently observed in the western subunit in March and April both years after WTD had dispersed. I hypothesize that the mere presence of high WTD densities deterred MD occupation of habitats in spatial zone 1 during early to mid-winter.

Other observations that supported this hypothesis were that MD and WTD shared habitats in spatial zone 4 at low densities during both winters. MD and WTD were also frequently observed feeding in large mixed groups (>40) in late winter. Also, individuals of both species were frequently observed feeding within 10 m of each other on sparsely forested slopes in late winter and early spring 1991-1993.

The possible exclusion of MD from spatial zone 1 by WTD probably had little if any effect in limiting the overall MD population on the BCWMA for the following reasons: (1) only a small portion of the MD population was influenced because MD had strong affinities for specific widespread wintering areas, and MD moved little during periods with low forage availability; (2) MD displayed no tendency toward movement into spatial zone 1 during severe weather; (3) MD were not observed at greater densities in habitats adjacent to spatial zone 1; (4) radio-collared MD exhibited no tendency to frequent areas near spatial zone 1 boundaries; (5) WTD excluded MD from an area where road-kill mortality was high, which might offset potential advantages to wintering MD in the absence of WTD; and (6) relatively low winter mortality and ample recruitment was observed for both deer species during 1992-1993. These 6 factors supported the conclusion that population limitation was minimal between MD and WTD. However, without further study the actual effects of MD exclusion by WTD remain unknown.

Winter Weather Conditions

Winter weather data indicated that crust conditions, snow depths and temperatures varied from site to site during both winters. Moreover, field observations suggested that site conditions often varied hourly and daily. When combined, weather variables provided an index for evaluating a site's ability to mitigate adverse influences of winter, and climatic stress to cervids caused by chilling and travel restriction (Verme 1968:566).

The capability of a site to mitigate severe winter conditions for cervids was dependent upon fixed variables. Fixed variables were those that remained relatively constant, such as overstory canopy cover, slope, aspect, elevation and neighboring topography. Non-fixed factors included weather variables that fluctuated daily, and their duration influenced winter harshness. Non-fixed weather variables included: temperature, snow accumulations, snow moisture, wind, rain and solar radiation. Sites with low winter severity both years were presumably those with structural and topographic characteristics that mitigated the greatest number of harsh weather variable combinations. Weather results indicated that sites with abundant overstory canopy cover possessed the greatest ability to mitigate potentially severe combinations of deep snow, crusted snow, cold temperatures and high wind.

Severe crust conditions observed in 1992 were promoted by deep persistent snow that accumulated in November and December 1991. Crust conditions in January and February 1992 were further elevated by mild daily temperatures, cold nighttime temperatures and freezing rain. Overstory canopy cover >50% did not substantially reduce snow crust under these conditions.

Although temperatures were colder and snow was deeper in 1993, stands with >29% overstory canopy cover generally had snow that was less crusted. Reduced snow crust probably decreased energy expenditures by cervids moving in these habitats (Verme 1968, Moen 1976, Parker et al. 1984). All 3 cervid species shifted use to habitats with greater overstory canopy cover as winter progressed and snow conditions worsened in 1993.

Various combinations of snow depth and crust characteristics can influence movement in snow by cervids (Verme 1968, Knight 1970:22, Parker et al. 1984). Physical movement through snow as deep as 100 cm on the BCWMA required little effort if snow was extremely light and powdery. WTD were observed frequently moving through snow as deep as 80 cm with little apparent effort under such conditions. In contrast, snow depths as low as 30 cm required great energy expenditure by the observer if a thin (2-4 cm) surface crust was present. As the influences of snow depth, snow crust and snow density intensified, resistance to movement increased until snow became hard enough to support an animal's weight (Verme 1968). Hard snow was observed infrequently on the BCWMA, and it was too variable to be of substantial benefit to cervids.

Although snow depth has commonly been considered a primary influence on winter habitat use by cervids, snow results for the BCWMA indicated that conditions could arise where crusted snow of lower depth could present a greater hardship to cervids than deeper non-crusted snow during cold periods. In order to more accurately estimate the influences of snow on cervid energy expenditures, it may be important to examine combinations of snow depth and crust conditions rather than snow depth alone (Verme 1968).

CHAPTER III: BROWSE PRODUCTION, UTILIZATION AND CONDITION

INTRODUCTION

Numerous studies have documented the importance of deciduous and evergreen shrubs as winter forage for elk, MD and WTD (Kufeld et al. 1973, Nelson and Leege 1982, Peek 1984). However, variability in forage abundance, availability, palatability, and animal numbers can complicate assessments of the relative importance of browse from one area to another (Kufeld 1973). Cervids that are highly dependent on browse in winter would presumably benefit most from productive and abundant shrubs that are available during severe winter conditions.

Browse was abundant on portions of the BCWMA. Observations of shrubs made in winter and spring by BCWMA managers suggested that use by elk, MD and WTD was often extreme (MDFWP survey notes, unpubl. data; M. A. Hurley, Univ. Idaho, Moscow, pers. commun.; M. J. Thompson, MDFWP, pers. commun.). Managers were concerned that long term overuse of shrubs by cervids would result in decreased browse vigor, leading to a reduction in current annual growth (CAG). Decreased browse production was expected to reduce cervid survival, especially during severe winters.

The potential for reduced shrub productivity caused by cumulative browsing by large numbers of elk, MD and WTD was unknown. Therefore, increased knowledge about the condition and abundance of browse on the BCWMA was needed to develop objectives for wintering numbers of elk, MD and WTD. This portion of the study was designed to:

1. Estimate browse production for snowbrush ceanothus (Ceanothus velutinus), chokecherry (Prunus virginiana), red-osier dogwood (Cornus stolonifera), Rocky Mountain maple (Acer glabrum), serviceberry, and scouler willow (Salix scouleriana) following 2 growing seasons.
2. Estimate browse utilization for the 6 shrub species following the corresponding two winters.
3. Document relative browse availability, mainstem decadence, growth form and mainstem replacement (sprouting potential) for the 6 shrub species.
4. Use the combined information to predict the effects of heavy utilization on the 6 shrub species, and subsequent winter survival prospects of cervids.

METHODS

Browse Production Sampling

Four CAG twig length classes were defined prior to establishing plots. Twigs of diverse lengths were clipped from shrubs across the study area, which were representative of various locations, aspects, elevations and growth forms. No more than 10 twigs were measured from any shrub. CAG twigs (n = 171-223) of each species were measured to the nearest mm. Twig lengths (n = 1,166) were plotted on a frequency histogram following Makela (1990). Length class ranges were based on clusters of twig lengths observed on the frequency histogram. The same length classes were used for all species during both years for tallying counted twigs observed on live shrubs.

While establishing transect segments (described in Chapter 1), 123 segments were determined to contain enough browse for sampling. Browse segments were later grouped into 4 general browse types based on similarity of slope and aspect.

Semi-permanent plots similar to those used by Makela (1990) were used in this study to improve precision of production and utilization estimates (P. D. Makela, U.S. Bur. Land Manage., pers. commun.). Semi-permanent browse plots were established (1 plot per segment) during initial browse production and condition sampling in September 1991. These plots were monitored to derive subsequent production and utilization estimates through May 1993. Plots were located perpendicular to browse segments according to the layout previously described (Fig. 4, Chapter 1). Twenty-eight browse plots were burned during the October 1991 wildfire leaving 95 for analysis. Analysis of burn effects was beyond the scope of this study.

Starting positions for browse plots were established at each segment midpoint. Each starting point was positioned 2 m perpendicular to a segment to minimize shrub trampling by the observer during winter track surveys. Plot direction (right or left of the transect at 70° or 250° azimuths) was determined by flipping a coin. Plot start and end locations were marked with steel stakes (1 cm diameter by 30 cm long).

A retractable 50 m measuring tape was positioned between the 2 stakes to measure plot length, and maintain the plot midline during twig counts. A 2 m measuring pole, with marked center, was moved perpendicularly along the tape to the distance necessary to encounter 100 CAG twigs or sprouts of the shrub species of interest. During the establishment of plots, the plot end stake was placed at the plot midline where the 100th twig was counted. Plot distance was measured to the nearest 0.1 m. Twigs on each plot were tallied by length class and species.

During second-year sampling (after plots were established) all twigs found within the plot boundary were tallied regardless of total. Counting also ceased during the second year when the end stake was reached.

Immediately following twig counts, CAG twigs were clipped from representative shrubs that grew 3-25 m from plot boundaries. When possible, all CAG twigs were clipped off 2-3 selected mainstems from at least 3 shrubs of each species observed in a plot vicinity. Leaves were stripped from all clipped twigs, except for those of snowbrush ceanothus. Ceanothus CAG was subjectively determined by leaf color and distance between nodes (Makela 1990). CAG twigs collected from mainstems were representative of growth in the four cardinal quadrants, shrub heights and growth forms observed at each plot vicinity. An effort was made to collect 20-30 twigs of each species and length class at each plot vicinity, but this was not always possible because of variations in species composition and density. Clipping all CAG from individual mainstems was expected to more accurately represent length proportions of natural-growing twigs, and mitigate potential twig collection biases such as those reported by Shafer (1963).

Twig samples were sorted by species, year, length class and browse type, and were oven-dried for 24 hr at 100° C (Lyon 1970). Sorted twigs were then weighed to the nearest 0.01 g.

Precipitation data for the 7-8 month period preceding production sampling for 1991 and 1992 were obtained for the Seeley Lake Ranger Station (Local Climatological Data, Natl. Weather Serv., Missoula, Mont.).

Data Analysis

Methods for calculating mean plot weight (g) and mean production per-unit-area (kg/ha) followed Makela (1990). Additional estimates of total kg sampled divided by total ha sampled were calculated for each browse type and combined browse types for both years.

Data were tested for normality by subjective inspection of a frequency histogram of residuals. Data were then log base e transformed (ln) and retested for normality and equal variance by examining normal probability plots and Levene tests respectively (Norusis 1988).

Student's paired *t*-test for samples with unequal variance was used to test the null hypothesis that mean plot weight (g) and mean kg/ha did not significantly differ for a browse type between years. One-way analysis of variance and the Tukey-b multiple comparisons test were used to test differences between means of 4 browse types within years (Norusis 1988).

Browse Utilization Sampling

Three, utilization methods were used during this study. First, twig weight-on-diameter relationships (Lyon 1970) were used to estimate dry weight removed from production plots post-winter. Second, post-winter estimates of percent CAG twigs browsed were obtained (Cole 1957a, as verified by Stickney 1966). Third, to compare the timing and relative browse use during both winters, 2 visual estimates per month of percent twigs browsed and mean twig length were recorded. This was done along each browse segment for the 6 species of interest during January, February and March 1992 and 1993. Twig length means by browse type were calculated for each month from combined segment means. Twig CAG diameter measurements and twig counts for utilization estimates were conducted similarly to production sampling, using established production plots.

Browsed CAG and previous year's growth (PYG) stem diameters were measured to the nearest 0.25 mm with a plastic dial caliper, and were recorded in one of seven above-ground height categories by species. Clipped CAG twigs obtained during production sampling were used for calculating species specific weight-on-diameter regression equations (Lyon 1970, Peek et al. 1971). Clipped twigs were oven-dried, measured and weighed following the methods of Lyon (1970). The square roots of weight values were used to construct regression equations that more closely fit weight-on-diameter distributions as described in Appendix F (S. K. Goering, Trinity Coll., pers. commun.).

Twigs were clipped 7 months before taking diameter measurements. Therefore, twig diameter shrinkage estimates were necessary so dry-twig subsample diameters would correspond with green browsed diameters measured in the field (L. J. Lyon, U. S. For. Serv., pers. commun.). Additional twigs were clipped (n = 679) from north and south aspects at various locations on the study area in order to derive mean shrinkage estimates. When possible, 20 twigs were clipped for each length class by species on north and south aspects. Twigs were individually numbered and measured within 24 hr after collection. Twigs were then oven dried for 24 hr at 100° C (Lyon 1970) and remeasured. Mean diameter shrinkage estimates were calculated by species and aspect for each of the 4 twig length classes, and were added to clipped-twig diameter data for deriving regression equations (L. J. Lyon, U. S. For. Serv., pers. commun.).

During utilization sampling in April 1992, numerous PYG stems were observed browsed across all shrub species and browse types. Cervid browsing of PYG stems was more severe than normal browsing of CAG twigs only (termed type 1 browsing) (Fig. 18). Browsed PYG stems (termed type 2 browsing) normally represented stem material 2-4 years old. Previously measured CAG twigs were consistently unaccounted-for on plots, which indicated that several CAG twigs had been browsed from one larger PYG stem (Fig. 18). Therefore, during 1993 utilization sampling, unbrowsed CAG twigs remaining on each plot were re-counted by species and lengthclass (following production methods). This weight estimate added to the weight estimate for browsed CAG twig diameters was used to estimate "accounted-for" twig weight for each plot. The assumption was made that cervids browsed twigs of various lengths in proportion to their occurrence on each plot.

Three general analytical techniques were used to estimate utilization weight: (1) estimates derived using CAG browsed twig diameters only (for 1992 and 1993), (2)

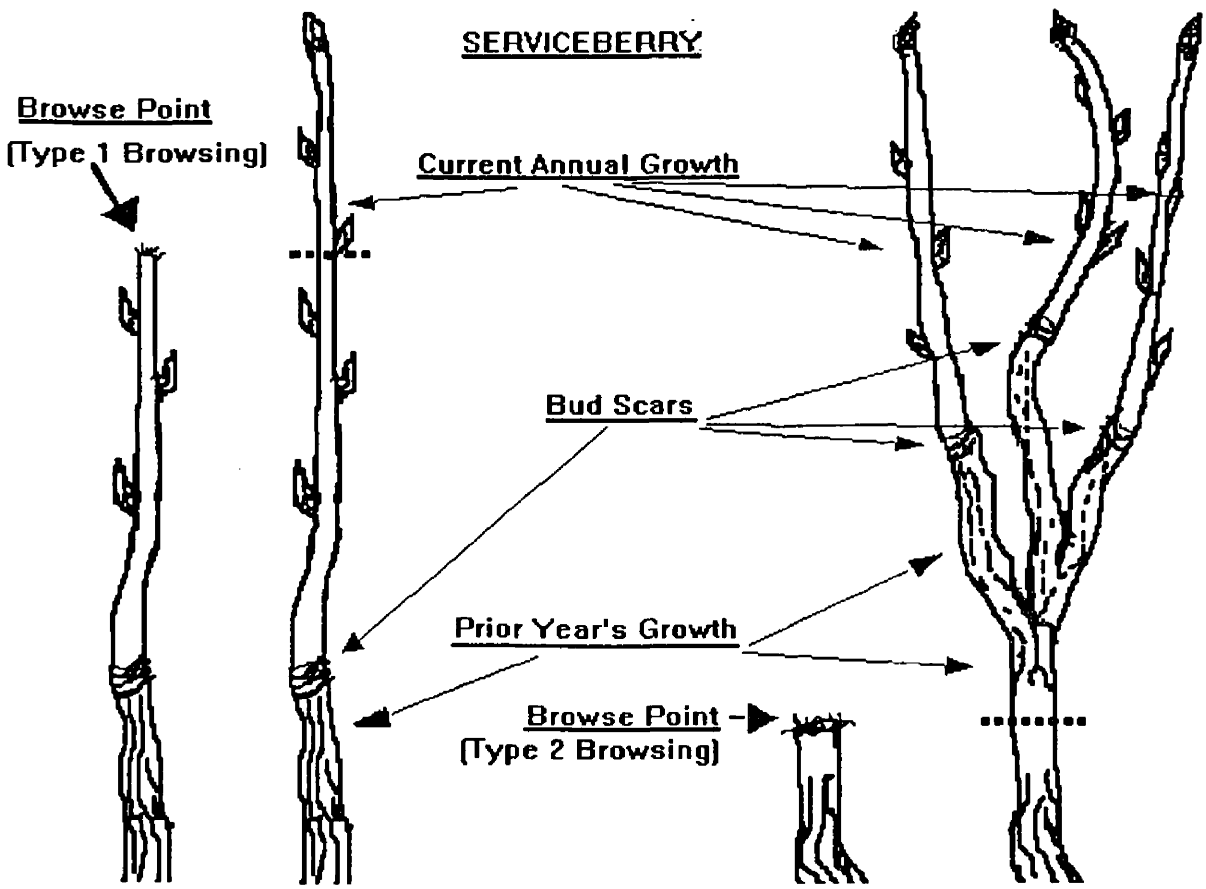


Figure 18. Diagram showing examples of serviceberry twigs before and after browsing. Type 1 browsing occurs when less than 100% of a current annual growth (CAG) twig is consumed, and a portion of CAG remains after browsing. Type 2 browsing occurs when 100% of one or several CAG twigs is consumed, and a browsed prior year's growth stem is all that remains. No evidence of CAG remains after type 2 browsing, therefore removed CAG twigs are "assumed" browsed or "unaccounted-for" twigs.

estimates that combined CAG browsed diameter and unaccounted-for CAG weight estimates (1993 only), and (3) inverse ln transformed means for combined diameter and unaccounted-for weight estimates (1993 only). Estimates were derived by calculating mean plot weights in g and kg/ha, and by using estimates of kg sampled divided by ha sampled for each type and types combined.

Data Analysis

Browsed twig diameter means were calculated for each plot by species using the formula provided in Appendix F (S. K. Goering, Trinity Coll., pers. commun.). Twig diameter means for each plot were entered into regression equations to obtain predicted twig weights (g). Regression equations were used to estimate CAG utilization from browsed CAG diameters only. Predicted twig weights were multiplied by the number of twigs browsed on a plot for each species and the products were summed. This produced a plot weight estimate. Plot weight estimates (g) were combined by browse type and means were calculated.

Plot weight estimates (g) were used to calculate utilization per-unit-area. Plot weight (g) was divided by plot area in m^2 and was converted to kg/ha. Plot kg/ha estimates were averaged by browse type and all types combined for 1992 and 1993.

The unaccounted-for CAG presumably utilized in 1993 as a result of type 2 browsing (Fig. 18), total weight utilization and % utilization were estimated using the following formulas:

$$A + B = C$$

$$D - C = E$$

$$E + A = F$$

$$(F/D)(100) = T$$

where A = CAG utilization plot weight (g) estimated from browsed twig diameters, B = weight of unbrowsed twigs (g) remaining on plot post-utilization, C = total accounted-for plot weight (g) post-utilization, D = 1992 production plot weight estimate (g), E = estimate of unaccounted-for CAG weight (g) removed as a result of type 2 browsing (Fig. 18), F = estimate of total plot weight (g) browsed, T = percent weight utilization estimate of production.

Estimates for total kg utilization divided by total ha sampled were calculated for each browse type and combined browse types for both years. Mean utilization plot data were tested for normality and ln transformed. Tests for significance within treatments between years and between treatments within years followed those of production methods. Student's paired *t*-test for samples with unequal variance was used to test for differences between CAG utilization estimates from browsed twig diameter data only, and total CAG utilization weight estimates (browsed diameter estimates + unaccounted-for twig weight estimates).

Difference in percentage of PYG stems browsed of all stems browsed between years was tested using the standard normal score for inferences of population proportions, and the difference between proportions of two samples (Johnson 1980:380).

Browse Condition and Summer Utilization Sampling

During browse plot establishment in summer 1991, visual estimates were made at each plot vicinity of % dead mainstems observed, % twigs browsed (i.e., summer utilization that occurred from about 15 May-15 August), shrub availability, and growth form class (Cole 1957b). Percentages of sprouts per 100 twigs were obtained from 1991 production counts. Results were summarized by browse type and for all types combined.

Cattle Influences

An assessment was made of serviceberry production on a partially forested shrub-field with 2 grazing treatments. One portion of the field had been rested from cattle grazing for 2 years, and an adjacent portion had been grazed seasonally for at least 30 years (M. J. Thompson, MDFWP, pers. commun.). Methods and results for shrub production and condition on these 2 sites are given in Appendix G.

RESULTS

Browse Production

Twig length classes (cm) established prior to twig counts were: short (2.0-14.9), medium (15.0-26.9), intermediate (27.0-41.9), and long (42.0+). Mean twig weights from clipped production samples for 1991 and 1992 are provided in Appendices H and I.

Serviceberry production (kg/ha) was consistently highest and upland willow lowest for the 6 shrubs of interest during 1991 and 1992 (Fig. 19). Serviceberry produced the most CAG for all site types, and Rocky Mountain maple was well represented on all types (Table 17). Chokecherry and ceanothus were primarily restricted to steep southerly exposures, while red-osier dogwood and upland willow favored flat or cool sites (Table 17). Weight estimates (g) for all species except red-osier dogwood were lower in 1992, and the weight sum for 1992 was 18.2% lower than for 1991 (Table 18).

The steep-south type produced the greatest mean plot weight (g) (a function of twig robustness in 1991, but robustness and abundance in 1992) (Table 19). However, the gentle-south type produced the greatest kg/ha (Table 20). Mean plot weight g was greater in 1991 on steep-north than gentle-north sites, however gentle-north was greater in 1992 (Table 19). This pattern was not observed in corresponding

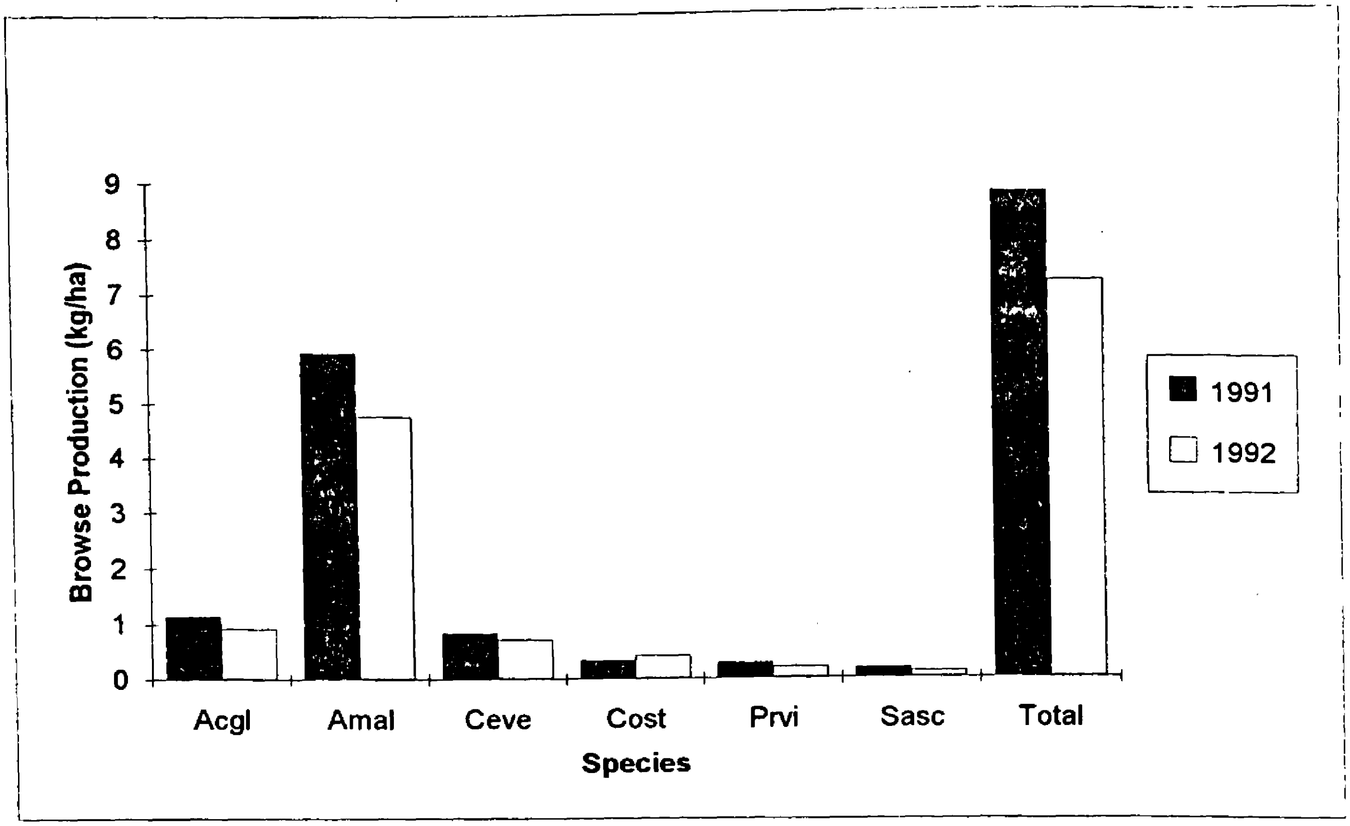


Figure 19. Contributions to total browse production (kg/ha) for six shrub species found on the BCWMA. Acgl = Rocky Mountain maple, Amal = Serviceberry, Ceve = Snowbrush ceanothus, Cost = Red-osier dogwood, Prvi = Chokecherry, Sasc = Scouler willow.

Table 17. Current annual growth (CAG) weight production for 6 shrub species sampled on 4 site types during 1991 and 1992 on the BCWMA. Percentages reflect species contributions to CAG browse weight for each site type.

	% CAG Browse Production by Weight							
	*Steep,S		*Steep,N		*Gentle,S		*Gentle,N	
Species [a]	1991	1992	1991	1992	1991	1992	1991	1992
Acgl	11.2	11.1	28.3	31.1	6.2	5.6	15.6	16.6
Amal	53.3	50.8	69.4	67.0	83.3	84.9	72.9	66.5
Ceve	26.6	29.7	0.0	0.0	0.0	0.0	0.0	0.0
Cost	0.0	0.0	0.0	0.0	7.9	7.2	7.5	14.1
Prvi	8.9	8.4	0.0	0.0	0.0	0.0	0.0	0.0
Sasc	0.0	0.0	2.3	1.9	2.6	2.3	4.0	2.8
Sum	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

a = Acgl = Rocky Mountain maple, Amal = Serviceberry, Ceve = Snowbrush ceanothus, Cost = Red-osier dogwood, Prvi = Chokecherry, Sasc = Scouler willow.

*Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.

Table 18. Current annual growth (CAG) production estimates (g) and percent contribution to total production (%) for 6 shrub species sampled on 95 plots on the BCWMA during 1991 and 1992. Weight estimates are plot sums for total grams sampled.

	1991		1992	
	CAG		CAG	
Species[a]	Weight Produced (g)	%	Weight Produced (g)	%
Acgl	238.1	13.2	191.5	13.0
Amal	1,223.3	68.0	979.8	66.6
Ceve	172.5	9.6	146.8	10.0
Cost	71.6	4.0	88.3	6.0
Prvi	57.9	3.2	41.7	2.8
Sasc	36.1	2.0	23.9	1.6
Sum	1,799.4	100.0	1,471.9	100.0

a = Acgl = Rocky Mountain maple, Amal = Serviceberry, Ceve = Snowbrush ceanothus, Cost = Red-osier dogwood, Prvi = Chokecherry, Sasc = Scouler willow.

Table 19. Mean plot weight estimates (g) for current annual growth of browse produced on the BCWMA during 1991 and 1992.

		1991			1992		
*Browse Type	n	Mean Plot Weight g (SD) [a]	ln Transformed Mean Plot Weight g (SD) [b]	ln Transformed 95% confidence Limits [b]	Mean Plot Weight g (SD) [a]	ln Transformed Mean Plot Weight g (SD) [b]	ln Transformed 95% confidence Limits [b]
Steep,S	25	25.95(16.3)	22.82(1.6)	18.8 to 27.8	19.80(17.2)	15.64(1.9)	11.9 to 20.5
Steep,N	14	15.96(7.3)	15.06(1.4)	12.6 to 18.1	10.30(5.7)	9.05(1.7)	6.7 to 12.2
Gentle,S	25	18.00(7.1)	16.64(1.5)	14.0 to 19.8	16.91(8.1)	14.70(1.8)	11.6 to 18.7
Gentle,N	31	15.38(7.4)	14.00(1.5)	12.0 to 16.4	13.23(9.0)	11.07(1.8)	8.9 to 13.7
all types	95	18.94(11.1)	16.90(1.6)	15.4 to 18.5	15.49(11.6)	12.68(1.9)	11.2 to 14.4

a = Non-transformed plot weight means and SDs.

b = Means, SDs and 95% confidence intervals were derived using ln transformed plot data (g). Given means, SDs and 95% confidence intervals are inverse ln values.

*Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
all types = all sites combined.

Table 20. Mean plot weight kg/ha estimates for current annual growth of browse produced on 4 site types during 1991 and 1992.

		1991				1992			
*Browse Type	n	Total kg/ha [a]	Mean Plot kg/ha (SD) [b]	ln Transformed Mean Plot kg/ha (SD) [c]	ln Transformed 95% confidence Limits [c]	Total kg/ha [a]	Mean Plot kg/ha (SD) [b]	ln Transformed Mean Plot kg/ha (SD) [c]	ln Transformed 95% confidence Limits [c]
Steep,S	25	9.62	31.93(68.4)	12.99(3.5)	7.8 to 21.7	7.34	26.58(61.6)	8.90(4.2)	4.9 to 16.1
Steep,N	14	5.96	21.46(31.9)	9.06(3.7)	4.3 to 19.1	3.84	10.43(12.7)	5.45(3.3)	2.7 to 10.9
Gentle,S	25	9.83	41.07(59.0)	18.15(3.9)	10.3 to 31.9	9.23	37.46(53.7)	16.03(4.2)	8.9 to 29.0
Gentle,N	31	8.57	25.88(35.1)	13.47(3.3)	8.7 to 20.8	7.37	24.73(48.4)	10.63(3.6)	6.7 to 17.0
all types	95	8.72	30.82(51.7)	13.61(3.5)	10.5 to 17.6	7.13	26.46(50.5)	10.24(4.0)	7.7 to 13.6

a = Estimate calculated as (Total kg produced/total ha sampled).
b = Non-transformed plot weight means and SDs.
c = Means, SDs and 95% confidence intervals were derived using ln transformed plot data (kg/ha). Given means, SDs and 95% confidence intervals are inverse ln values.

*Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
all types = all sites combined.

kg/ha results (Table 20).

In comparing analytical methods, mean plot weights (g) and inverse ln transformed mean estimates were comparable; however, transformed means were consistently lower (Table 19). Total kg/ha estimates calculated as kg produced/ha sampled were substantially lower than mean plot kg/ha estimates by type and all types combined (Table 20). Total estimates were also considerably lower than inverse ln transformed means (Table 20).

Inverse ln transformed mean plot weights (g) and mean plot kg/ha were significantly different between years for each type ($P < 0.05$) except gentle-south (Figs. 20 and 21). Significant differences between years were also observed ($P < 0.05$) for all types combined (Figs. 20 and 21).

The steep-south type had a greater mean plot weight (g) than all other types in 1991 ($P < 0.05$), but it exceeded only the steep-north type in 1992 (Fig. 22). Significant differences between types ($P < 0.05$) for mean kg/ha estimates were not observed in 1991 or 1992 (Fig. 23).

Precipitation data obtained for 1991 and 1992 indicated that more moisture accumulated prior to production sampling in 1991 than 1992 (Fig. 24). Therefore, the 1991 kg/ha estimate weighted by the area sampled (8.72 ± 2.17, $n = 95$) ($\bar{x} = \pm$ 95% CI) was the most reasonable estimate for normal precipitation years.

Estimates of shrub-forage days indicated that browse

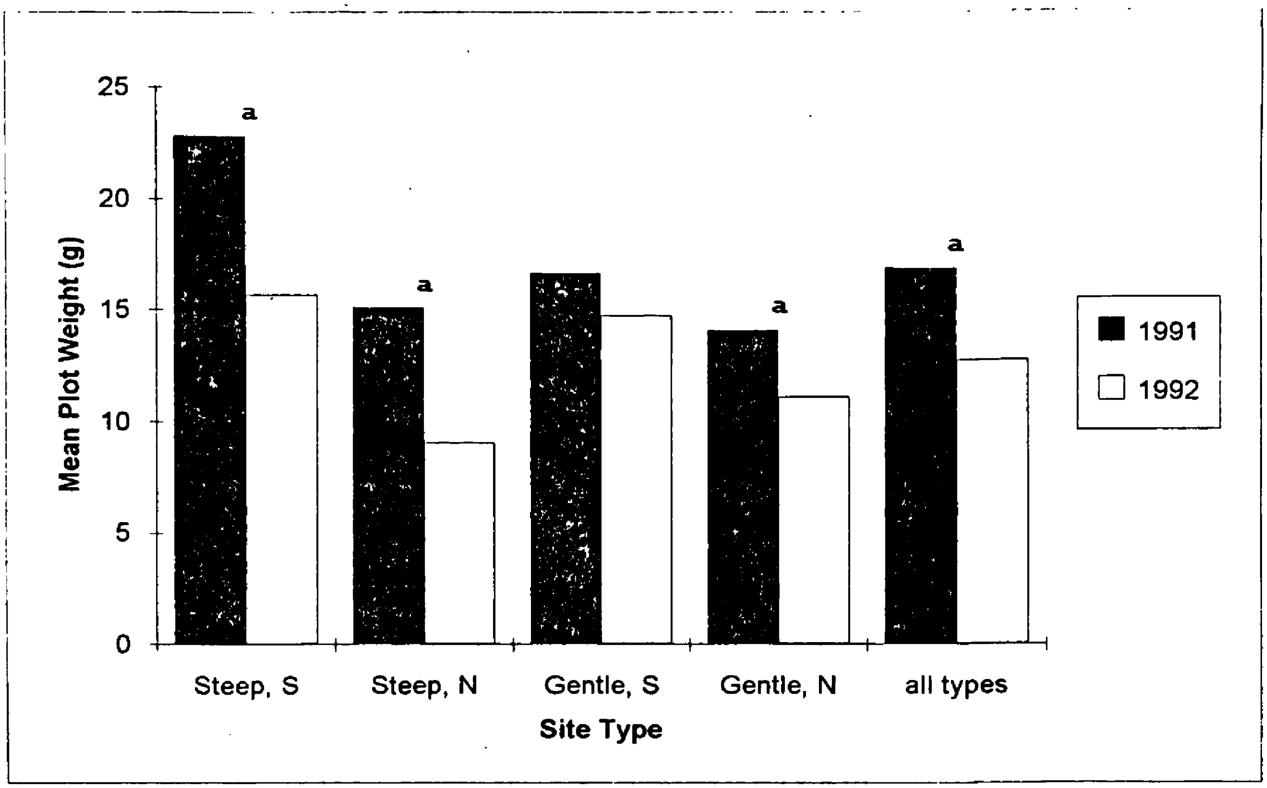


Figure 20. Comparison of browse production mean plot weights (g) between years for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Means were derived using ln transformed plot data. Reported means are inverse ln values. a = pairs differ significantly ($P < 0.05$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
all types = all site types combined.

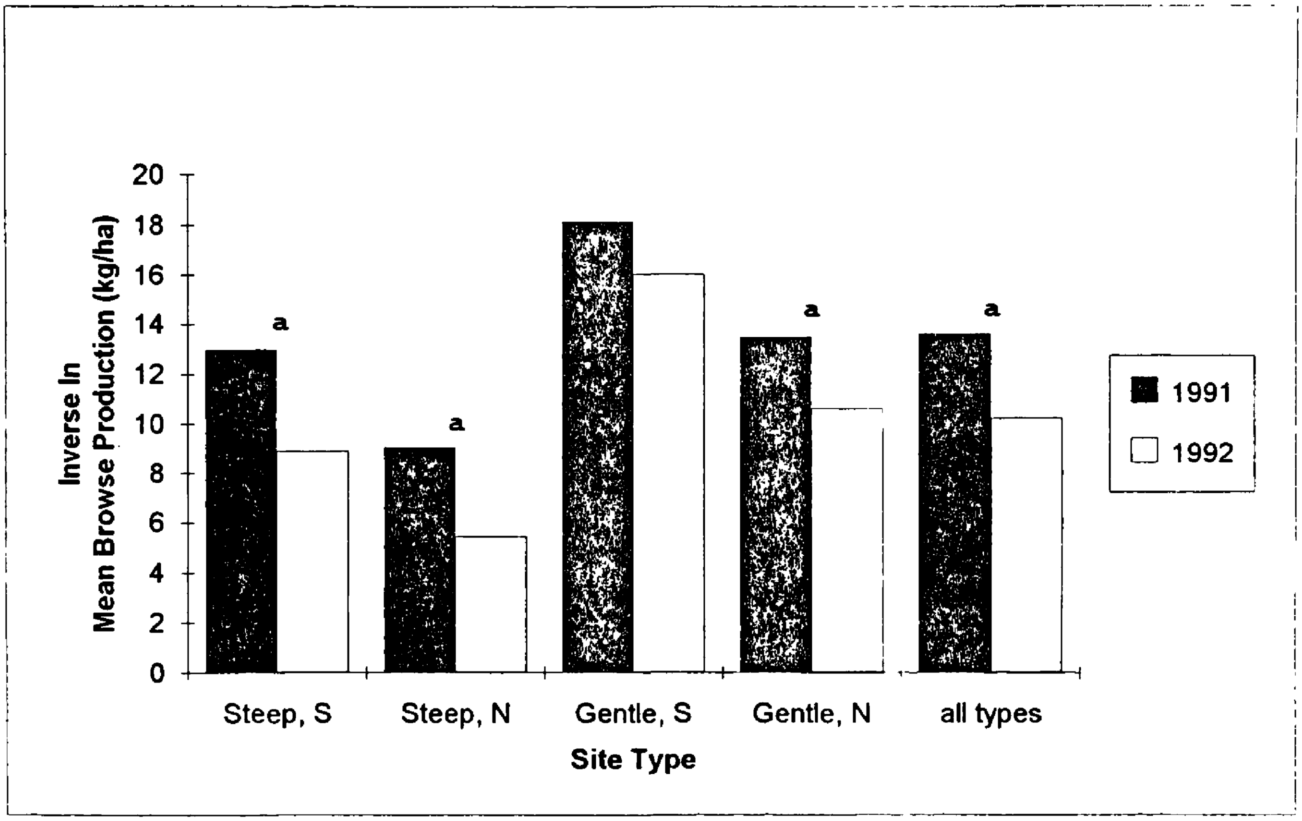


Figure 21. Comparison of browse production mean plot kg/ha between years for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Means were derived using ln transformed plot data. Reported means are inverse ln values. a = pairs differ significantly ($P < 0.05$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
all types = all site types combined.

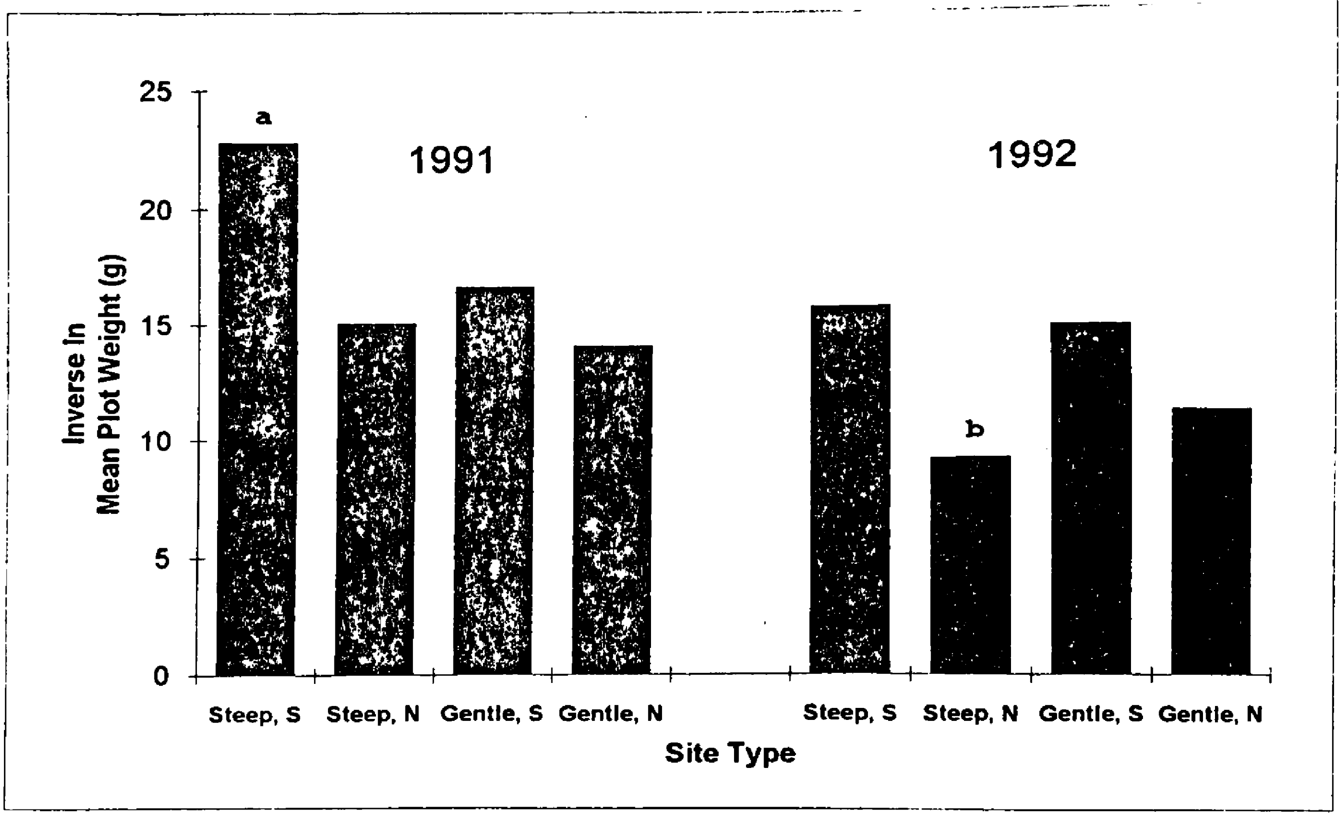


Figure 22. Comparison of browse production mean plot weight (g) between site types, within years for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Means were derived using ln transformed plot data. Reported means are inverse ln values. a = browse type significantly different than all other types in 1991 ($P < 0.05$). b = type significantly different than Steep,S type in 1992 ($P < 0.05$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
all types = all site types combined.

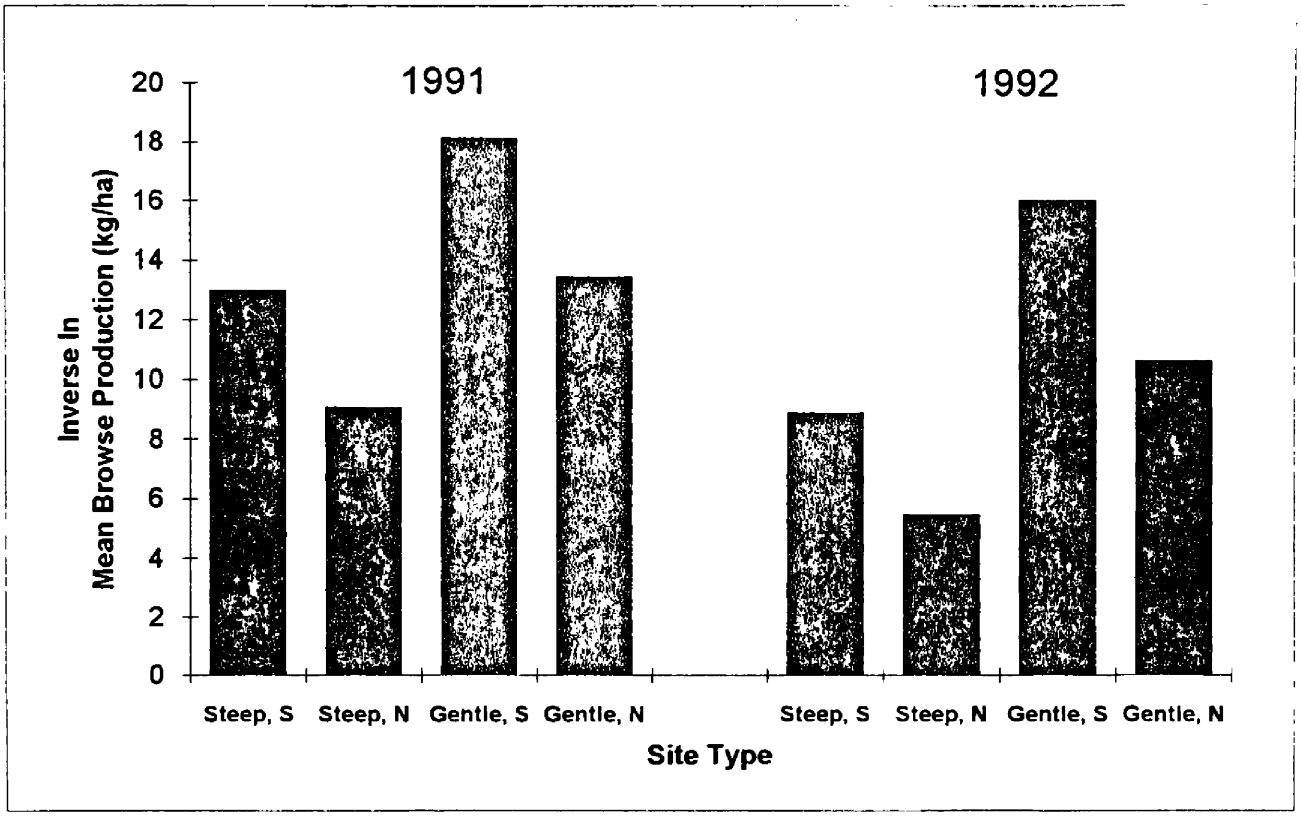


Figure 23. Comparison of browse production mean plot kg/ha between site types, within years for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Means were derived using ln transformed plot data. Reported means are inverse ln values. No types were significantly different in 1991 or 1992 ($P > 0.05$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
all types = all site types combined.

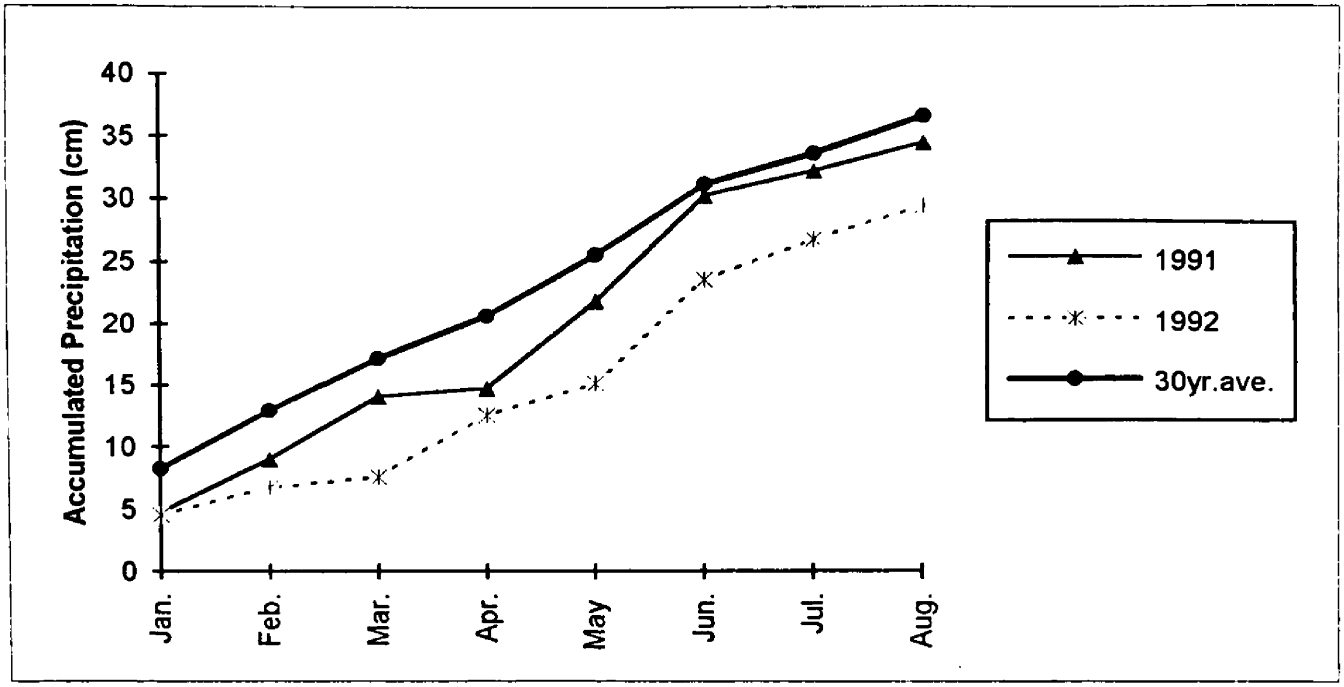


Figure 24. Accumulated precipitation at Seeley Lake Ranger Station for the 8 months prior to browse production sampling on the BCWMA (Local Climatological Data, Natl. Weather Serv., Missoula, Mont.). Total January-August precipitation was 5.8% below normal for 1991 and 19.6% below normal for 1992.

CAG would provide sole forage for the 3 cervid populations for about 9 days (Table 21). Additional shrub-forage day estimates for elk, MD and WTD are included in Appendix J.

Browse Utilization

Visual estimates of percent leaders browsed for the 6 shrub species of interest during early January 1992 were greater than those observed during early January 1993. Visual utilization estimates for site type 1 were consistently greater than for other types (Figs. 25 and 26). Increasing trends in percent leaders browsed for each site type were observed in 1993, which were not apparent in 1992 (Figs. 25 and 26). March estimates for percent leaders browsed were greater than 49% for all site types during both years, and sample variability reflected differential foraging intensities observed across segments (Figs. 25 and 26). Percent browsed leader estimates for March were less than late February estimates for types 1 and 3 in 1992, and types 1, 3, and 4 in 1993 (Figs. 25 and 26).

Trends in visual estimates of twig length were similar to those of percent twigs browsed. Expected decreasing trends in twig length were less obvious in 1992 than in 1993, and increases in length were observed from late February-March 1992 for all types (Figs. 27 and 28). Browsed and unbrowsed twigs from 6-10 cm were common on most sites throughout both winters, and mean length reductions

Table 21. Estimates of number of elk, mule deer (MD) and white-tailed deer (WTD) days at approximated population levels from 1991-1993. Current annual growth (CAG) from 6 browse species was assumed to be the sole forage resource, to have equal palatability, and to be 100% available in winter on the BCWMA.

Elk consume 4.1 kg/day deciduous browse (for a 225 kg adult cow) (Geis 1954).
Mule deer consume 1.3 kg/day deciduous browse (for a 54 kg adult doe) (Smith 1959).
White-tailed deer consume 1.6 kg/day deciduous browse (for a 45 kg adult doe) (Dahlberg and Guettinger 1956)

Estimate of browse type area estimated from DelSordo (1993) = 6,496 ha.

Daily Consumption
1,000 elk x 4.1 = 4,100 kg/day.
1,000 MD x 1.3 = 1,300 kg/day.
500 WTD x 1.6 = 800 kg/day.
Total = 6,200 kg/day.

Total Production 1991 = 8.72 kg/ha (with average precipitation during the growing season).

6,496 ha x 8.72 kg = 56,645.1 total kg produced in year 1991.

Total number of browse forage days for all cervids assuming 100% CAG utilization (non-sustainable).
Elk, MD and WTD: 56,645.1/6,200 kg = 9.14 days

Total number of browse forage days for all cervids incorporating 50% proper use value (sustainable).
Elk, MD, and WTD: (56,645.1 x 0.5)/6,200 kg = 4.57 days

Forage requirements for 3.8% of 120 winter days (ie. (4.57/120) x 100) could be met by the 6 studied browse species.

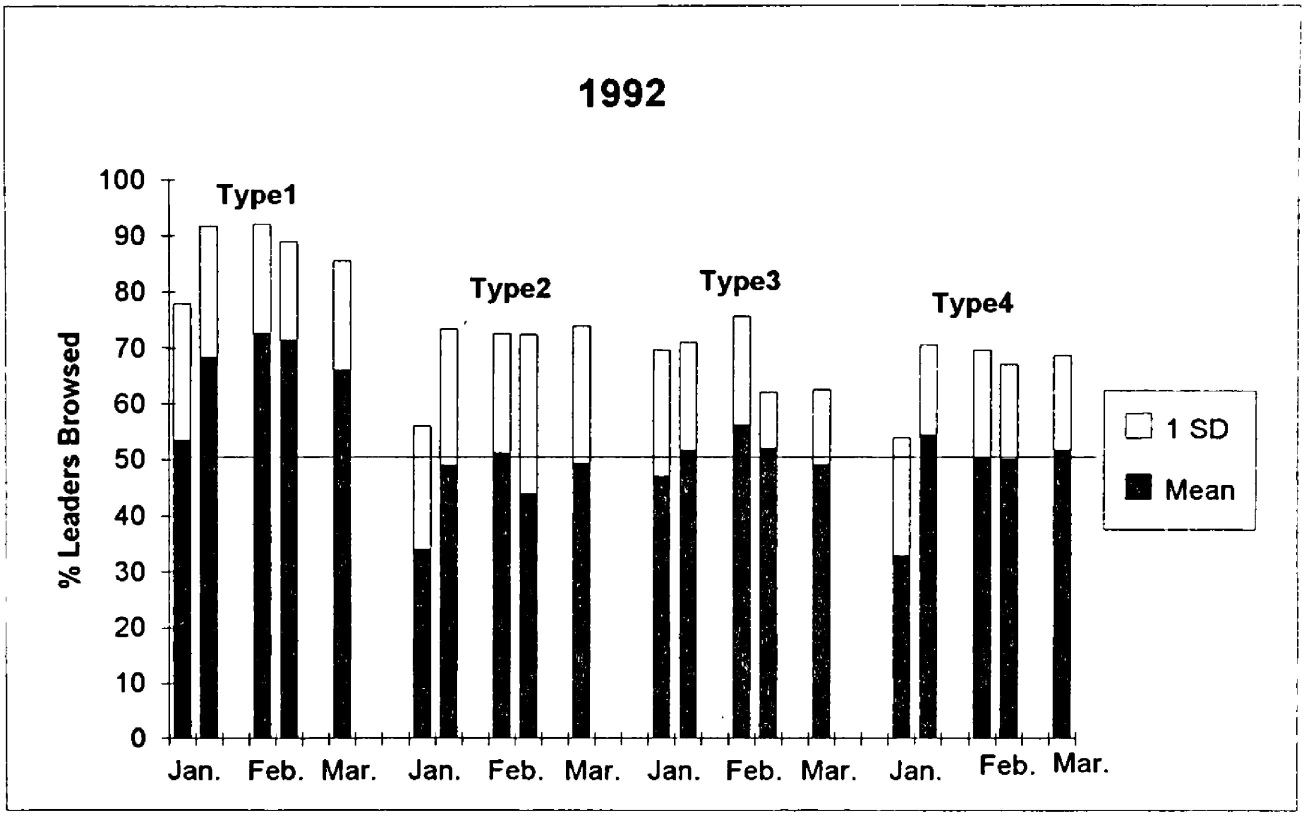


Figure 25. Mean percent leaders browsed during winter 1992. Horizontal reference line indicates 50% utilization level. Type 1 = stands with >20% slope, southerly exposure. Type 2 = stands with >20% slope, northerly exposure. Type 3 = stands with <20% slope, southerly exposure. Type 4 = stands with <20% slope, northerly exposure.

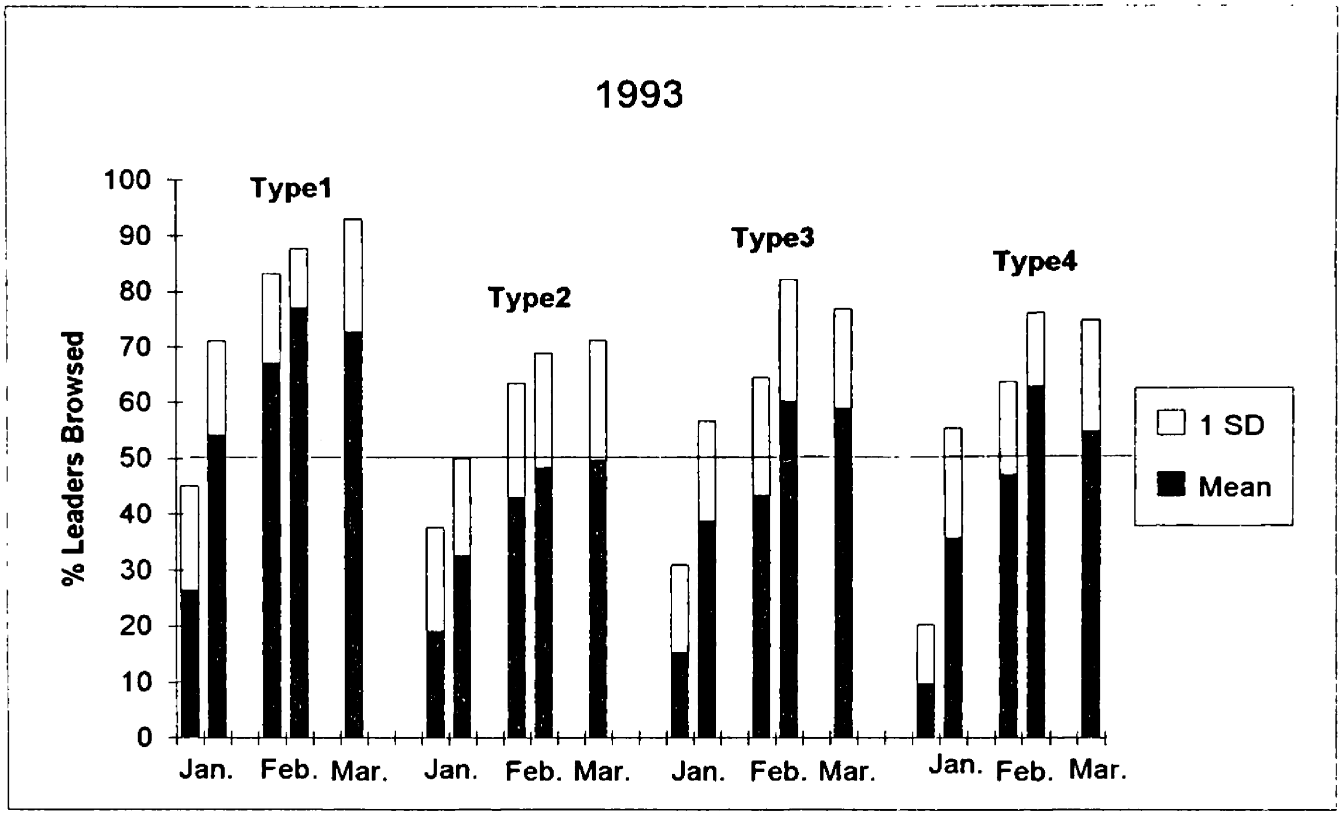


Figure 26. Mean percent leaders browsed during winter 1993. Horizontal reference line indicates 50% utilization level. Type 1 = stands with >20% slope, southerly exposure. Type 2 = stands with >20% slope, northerly exposure. Type 3 = stands with <20% slope, southerly exposure. Type 4 = stands with <20% slope, northerly exposure.

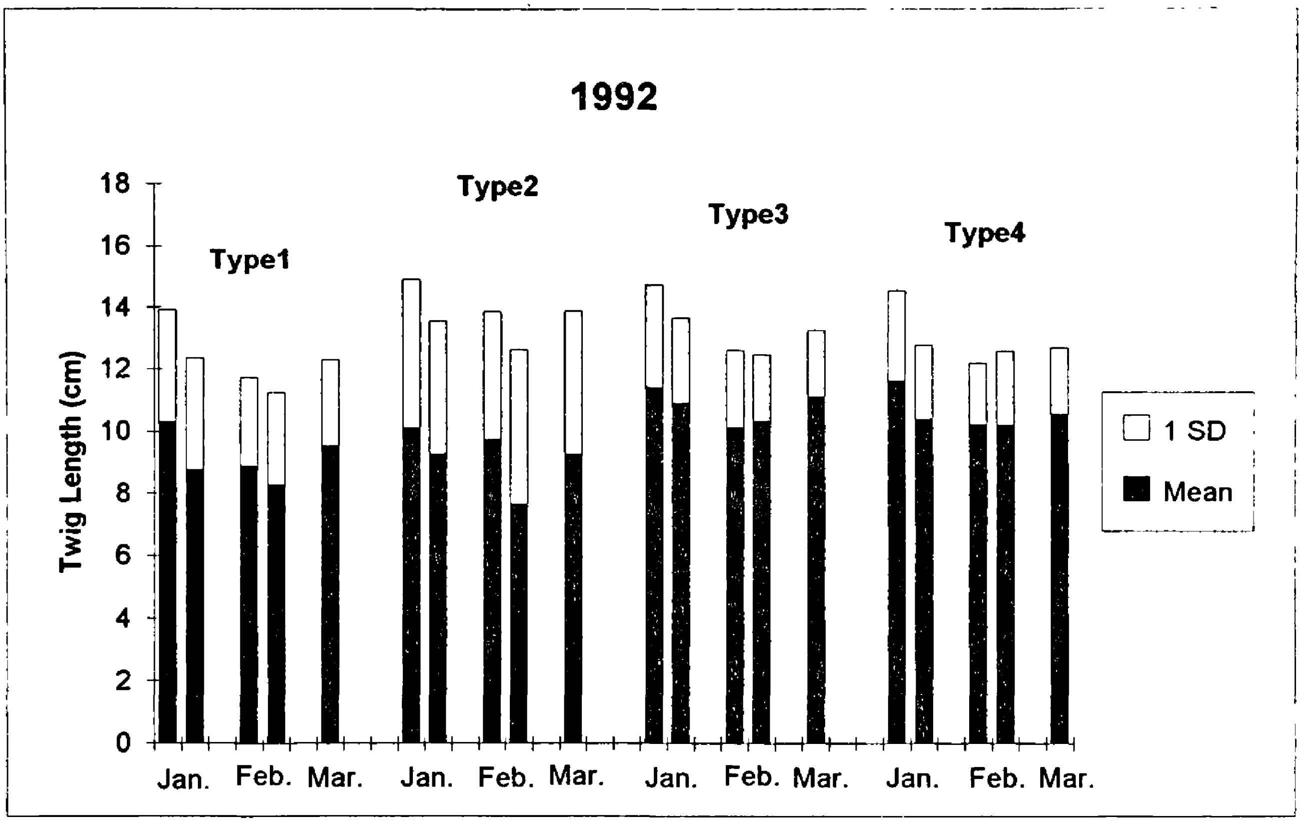


Figure 27. Mean twig lengths (cm) observed during winter 1992. Type 1 = stands with >20% slope, southerly exposure. Type 2 = stands with >20% slope, northerly exposure. Type 3 = stands with <20% slope, southerly exposure. Type 4 = stands with <20% slope, northerly exposure.

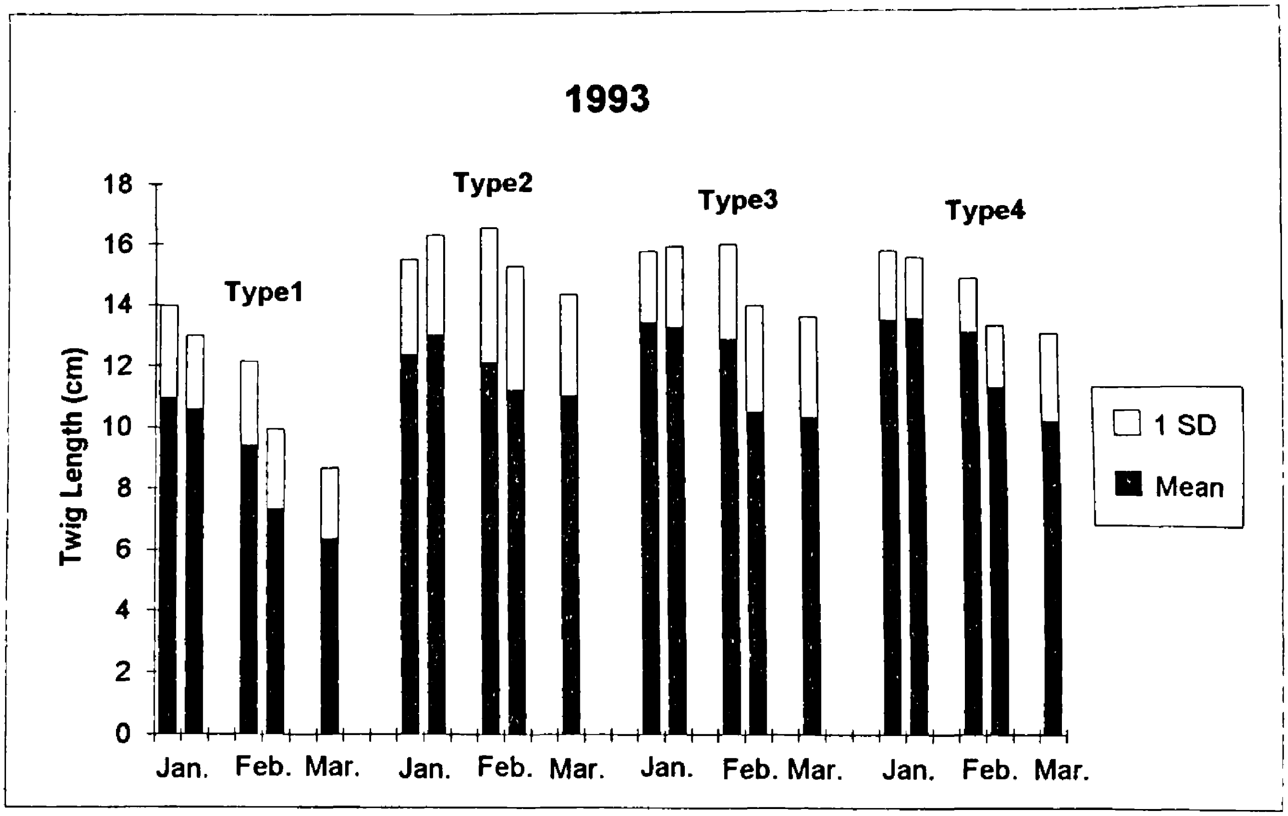


Figure 28. Mean twig lengths (cm) observed during winter 1993. Type 1 = stands with >20% slope, southerly exposure. Type 2 = stands with >20% slope, northerly exposure. Type 3 = stands with <20% slope, southerly exposure. Type 4 = stands with <20% slope, northerly exposure.

from January-March never exceeded 50% (Figs. 27 and 28).

Trends in percent leaders browsed and mean twig lengths for all types combined by month were similar to non-combined results (Figs. 29 and 30). Means and standard deviations for percent leaders browsed and mean twig lengths are provided in Appendices K and L.

Post-winter twig counts for CAG browsed diameters were considerably lower for the 6 species than estimates that included unaccounted-for twigs that were assumed browsed (Tables 22 and 23). Unaccounted-for twig percentages tended to be greater in 1992; however, percentages of prior year's growth stems browsed were greater in 1993 (Table 24).

Results for post-winter browsed twig counts in 7 above-ground height classes indicated that cervids made greatest use of shrubs from 0-91.5 cm tall, and 91% of all browsed CAG twigs were encountered below 122 cm (Fig. 31). Summaries of counts and percentages of CAG browsed twigs by species and height class are provided in Appendix M.

Diameter shrinkage means for clipped twig samples were all less than 0.81 mm for all length classes, and were greater for south aspects than for north (Appendix N). Twig length shrinkage means were also calculated (Appendix O). Regression equations derived for estimating CAG utilization weight from browsed twig diameters in 1991 and 1992 were distinct, but maintained R^2 ranges of 0.84-0.94 and 0.89-0.95 respectively (Table 25).

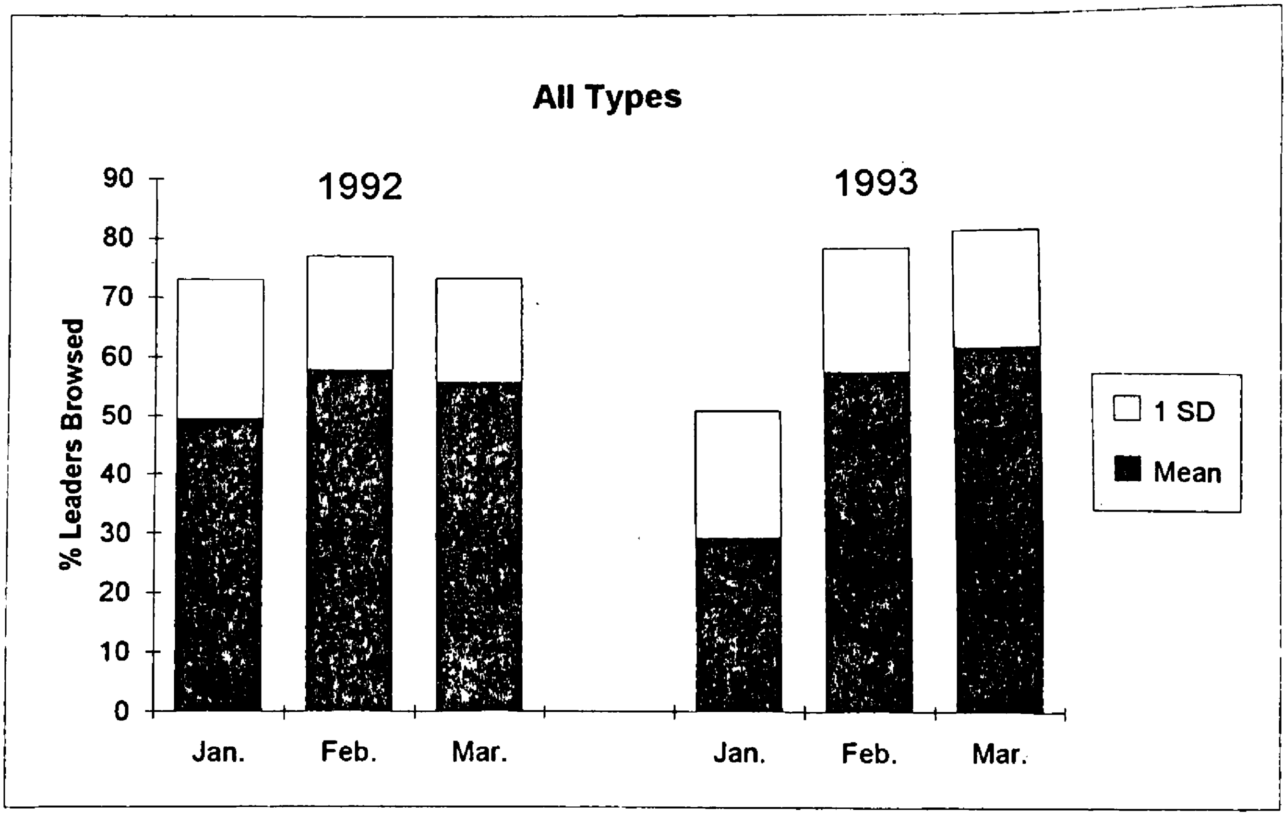


Figure 29. Mean percent leaders browsed for all sites during winters of 1992 and 1993 (visual estimates).

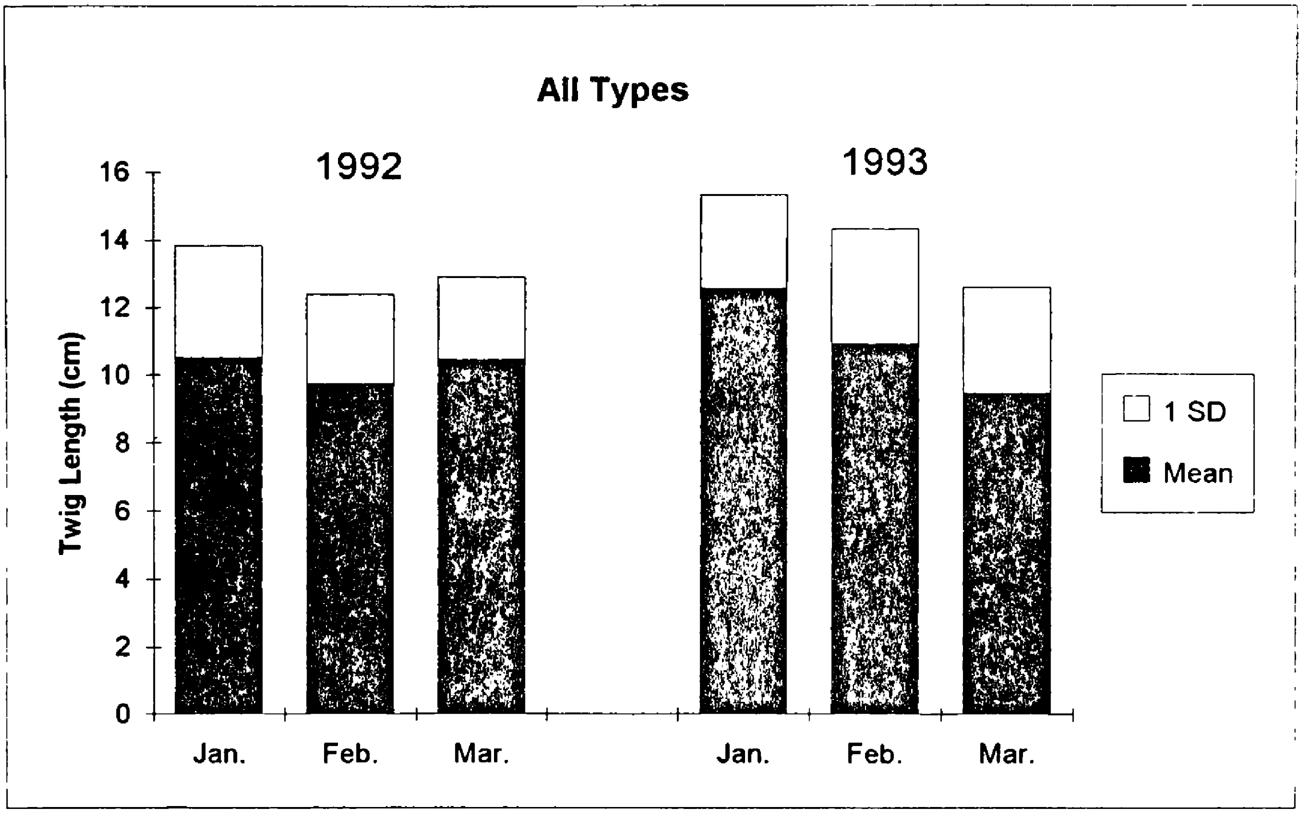


Figure 30. Mean twig length (cm) for all sites during winters of 1992 and 1993 (visual estimates).

Table 22. Number of current annual growth (CAG) twigs counted during production sampling (CAG Produced), number of CAG browsed twigs observed post-winter (CAG Browsed), and percentages of CAG browsed diameters (% CAG Browsed) observed during utilization sampling conducted April-May on the BCWMA.

Species	1991 CAG Produced	1992 CAG Browsed	1992 CAG Produced	1993 CAG Browsed	1992 % CAG Browsed	1993 % CAG Browsed
Acgl	1,293	414	942	194	32.0	20.6
Amal	8,994	1,932	5,785	1,158	21.5	20.0
Ceve	488	73	194	91	15.0	46.9
Cost	420	129	443	88	30.7	19.9
Prvi	277	116	196	109	41.9	55.6
Sasc	701	182	291	81	26.0	27.8
Total	12,173	2,846	7,851	1,721	23.4	21.9

Acgl = Rocky Mountain maple
Amal = Serviceberry
Ceve = Snowbrush ceanothus
Cost = Red-osier dogwood
Prvi = Chokecherry
Sasc = Scouler willow

Table 23. Percentage estimates for the number of current annual growth (CAG) twigs browsed during winters 1992 and 1993 on the BCWMA. Estimates were derived from plot counts of CAG browsed diameters, remaining unbrowsed CAG twigs, and total twigs known to be present at time of production sampling.

Species	1992 % Browsed	1993 % Browsed
Acgl	51.8	45.0
Amal	47.1	35.7
Ceve	51.7	46.9
Cost	45.7	31.8
Prvi	84.8	76.5
Sasc	73.3	46.7
Total	51.3	37.9

Acgl = Rocky Mountain maple
Amal = Serviceberry
Ceve = Snowbrush ceanothus
Cost = Red-osier dogwood
Prvi = Chokecherry
Sasc = Scouler willow

Table 24. Percentage estimates for the number of current annual growth (CAG) twigs browsed that were unaccounted for (% Unacc.) as a result of cervid browsing beyond CAG, and percentages of previous year's growth (%PYG) stems browsed as a percentage of all stems observed browsed during winters 1992 and 1993. Estimates were derived from plot counts of CAG browsed diameters, remaining unbrowsed CAG twigs, browsed prior year's growth stems, and total twigs known to be present at time of production sampling.

Species	1992 % Unacc.	1993 % Unacc.	1992 % PYG	1993 % PYG
Acgl	19.8	24.4	20.3	29.5
Amal	25.6	15.7	28.9	46.1
Ceve	36.7	*-15.5	3.9	11.7
Cost	15.0	11.9	15.6	24.8
Prvi	42.9	20.9	32.6	32.7
Sasc	47.3	18.9	9.5	23.6
Total	27.9	16.0	25.8	40.9

Acgl = Rocky Mountain maple
Amal = Serviceberry
Ceve = Snowbrush ceanothus
Cost = Red-osier dogwood
Prvi = Chokecherry
Sasc = Scouler willow

* snow bent "new" ceve stems into plot causing a net increase in CAG twigs.

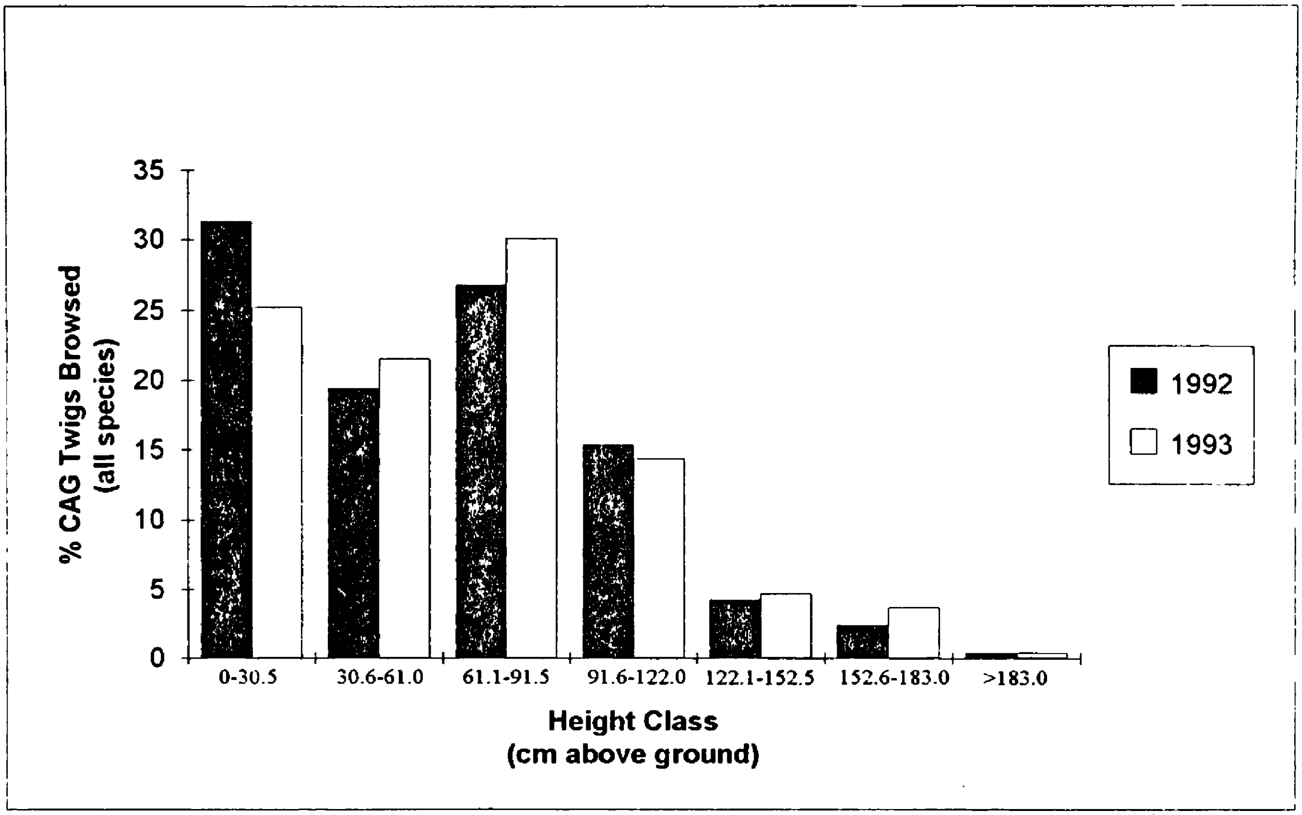


Figure 31. Percentages of current annual growth twigs browsed in 7 above-ground height classes during the winters of 1992 and 1993. Greater than 91% of all CAG browsed twigs were encountered below 122 cm for both winters.

Table 25. Regression equations (derived from twigs collected during August and September of 1991 and 1992) for estimation of twig weight removed from browsed current annual growth twig diameters measured during spring 1992 and 1993.

	Year 1991			Year 1992		
Species[a]	n	R^2		n	R^2	
Acgl	293	0.93	$est.wt.(g)=[-0.426+0.437(dia.mm)]^2$	309	0.95	$est.wt.(g)=[-0.506+0.471(dia.mm)]^2$
Amal	315	0.93	$est.wt.(g)=[-0.603+0.483(dia.mm)]^2$	312	0.94	$est.wt.(g)=[-0.648+0.504(dia.mm)]^2$
Ceve	133	0.84	$est.wt.(g)=[-0.312+0.486(dia.mm)]^2$	98	0.89	$est.wt.(g)=[-0.483+0.564(dia.mm)]^2$
Cost	118	0.91	$est.wt.(g)=[-0.432+0.424(dia.mm)]^2$	139	0.95	$est.wt.(g)=[-0.515+0.450(dia.mm)]^2$
Prvi	115	0.91	$est.wt.(g)=[-0.546+0.427(dia.mm)]^2$	63	0.94	$est.wt.(g)=[-0.480+0.406(dia.mm)]^2$
Sasc	233	0.94	$est.wt.(g)=[-0.383+0.420(dia.mm)]^2$	296	0.94	$est.wt.(g)=[-0.428+0.420(dia.mm)]^2$

a = Acgl = Rocky Mountain maple, Amal = Serviceberry, Ceve = Snowbrush ceanothus, Cost = Red-osier dogwood, Prvi = Chokecherry, Sasc = Scouler willow.

Mean plot weights (g) and (kg/ha), and kg sampled/ha sampled estimates for browsed diameter data are given in (Tables 26 and 27). Mean plot weight estimates (g) calculated from browsed diameters were significantly different ($P < 0.05$) between years for the steep-north type only (Fig. 32). No significant differences were observed ($P > 0.05$) for utilization estimates (kg/ha) between years for browsed twig diameter data (Fig. 33).

Utilization estimates for 1993 that combined browsed diameter weights and unaccounted-for twig weights were consistently greater than weight estimates derived from browsed diameters only (Tables 26 and 27). Differences were significant ($P < 0.001$) for mean plot weights (g and kg/ha) across all types (Figs. 34 and 35).

Lower utilization was observed ($P < 0.05$) on the steep-north type for 1993 comparisons of combined diameter and unaccounted-for weight estimates (Figs. 36 and 37).

All utilization by weight estimates for 1992 and 1993 were greatest for browse types with southerly exposures, and estimates for the steep-north type were lowest (Tables 26 and 27).

The 3 general analysis methods (kg sampled/ha sampled, inverse ln transformed mean plot weights, and mean plot weights) gave low, medium and high estimates respectively (Tables 26 and 27). The 1993 total kg/ha CAG utilization estimates were expected to be comparable with mean plot

Table 26. Browse utilization weight estimates (g) for current annual growth (CAG) removed from 95 browse plots on the BCWMA during winters 1992 and 1993.

		1 9 9 2	1 9 9 3			
*Browse Type	n	Mean Plot CAG g (SD) [a]	Mean Plot CAG g (SD) [b]	Mean Plot Total g (SD) [c]	ln Transformed Mean Plot Total g (SD) [d]	ln Transformed 95% confidence Limits [d]
Steep,S	25	5.02(6.1)	3.90(4.0)	11.33(10.1)	7.28(3.0)	4.7 to 11.4
Steep,N	14	1.47(1.6)	0.97(1.6)	3.51(4.4)	1.10(17.7)	0.2 to 5.8
Gentle,S	25	3.47(3.5)	3.60(4.1)	9.53(7.5)	4.91(7.8)	2.1 to 11.5
Gentle,N	31	1.98(1.8)	1.76(2.8)	6.10(7.1)	3.84(2.8)	2.6 to 5.6
All types	95	3.10(4.0)	2.69(3.5)	8.00(8.2)	4.03(6.0)	2.8 to 5.8

a = Plot weight estimates (g) used for mean calculations. Weight estimates from 1992 CAG diameters only.

b = Plot weight estimates (g) used for mean calculations. Weight estimates from 1993 CAG diameters only.

c = Plot weight estimates (g) used for mean calculations. Weight estimates were obtained from combined 1993 CAG twig diameter weight estimates and unaccounted for CAG twig weight estimates represented by browsed coarse prior year's growth stems.

d = Means, sds and 95% confidence intervals were derived using ln transformed plot data (g). Given means, sds and 95% confidence intervals are inverse ln values.

*Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

Table 27. Browse utilization weight estimates (kg/ha) for current annual growth (CAG) removed from 95 browse plots on the BCWMA during winters 1992 and 1993.

		1992		1993					
*Browse Type	n	CAG kg/ha [a]	Mean Plot CAG kg/ha (SD) [b]	CAG kg/ha [c]	Mean Plot CAG kg/ha (SD) [d]	Total kg/ha [e]	Mean Plot Total kg/ha (SD) [f]	ln Transformed Mean Plot Total kg/ha (SD) [g]	ln Transformed 95% confidence Limits [g]
Steep,S	25	1.9	13.0(52.9)	1.5	6.1(17.2)	4.2	19.0(55.7)	4.1(5.9)	2.0 to 8.6
Steep,N	14	0.6	1.8(3.0)	0.4	0.9(2.1)	1.3	3.9(7.1)	0.6(19.3)	0.1 to 3.2
Gentle,S	25	1.9	8.2(17.7)	2.0	8.8(19.0)	5.2	22.0(38.4)	5.4(11.3)	2.0 to 14.6
Gentle,N	31	1.1	3.5(5.5)	1.0	3.2(8.0)	3.4	10.7(23.3)	3.7(4.6)	2.1 to 6.5
All types	95	1.4	7.0(28.7)	1.2	5.1(14.0)	3.7	14.8(37.3)	3.2(8.9)	2.0 to 5.0

a = Total weight estimate/total area sampled (kg/ha). Weight estimates from 1992 CAG diameters only.

b = Plot weight estimates (kg/ha) used for mean calculations. Weight estimates from 1992 CAG diameters only.

c = Total weight estimate/total area sampled (kg/ha). Weight estimates from 1993 CAG diameters only.

d = Plot weight estimates (kg/ha) used for mean calculations. Weight estimates from 1993 CAG diameters only.

e = Total weight estimates/total area sampled (kg/ha). Weight estimates were obtained from combined 1993 CAG twig diameter weight estimates and unaccounted for CAG twig weight estimates represented by browsed coarse prior year's growth stems.

f = Plot weight estimates (kg/ha) used for mean calculations. Weight estimates were obtained from combined 1993 CAG twig diameter weight estimates and unaccounted for CAG twig weight estimates represented by browsed coarse prior year's growth stems.

g = Means, sds and 95% confidence intervals were derived using ln transformed kg/ha plot data. Given means, sds and 95% confidence intervals are inverse ln values.

*Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

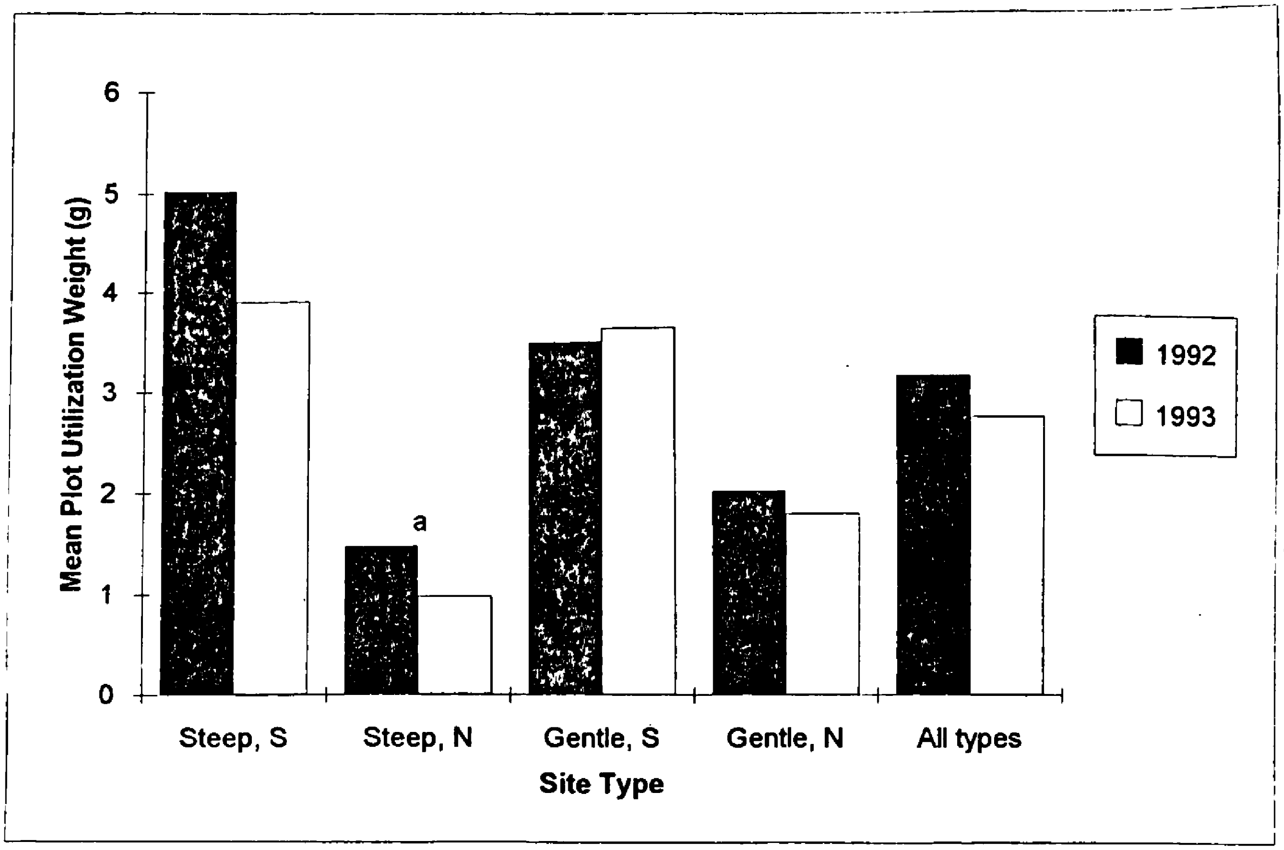


Figure 32. Current annual growth (CAG) mean plot utilization weight (g) for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Estimates were derived from CAG diameter data only. Plot data were ln transformed and means were tested for significance. a = significant difference in means between years was observed ($P < 0.05$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

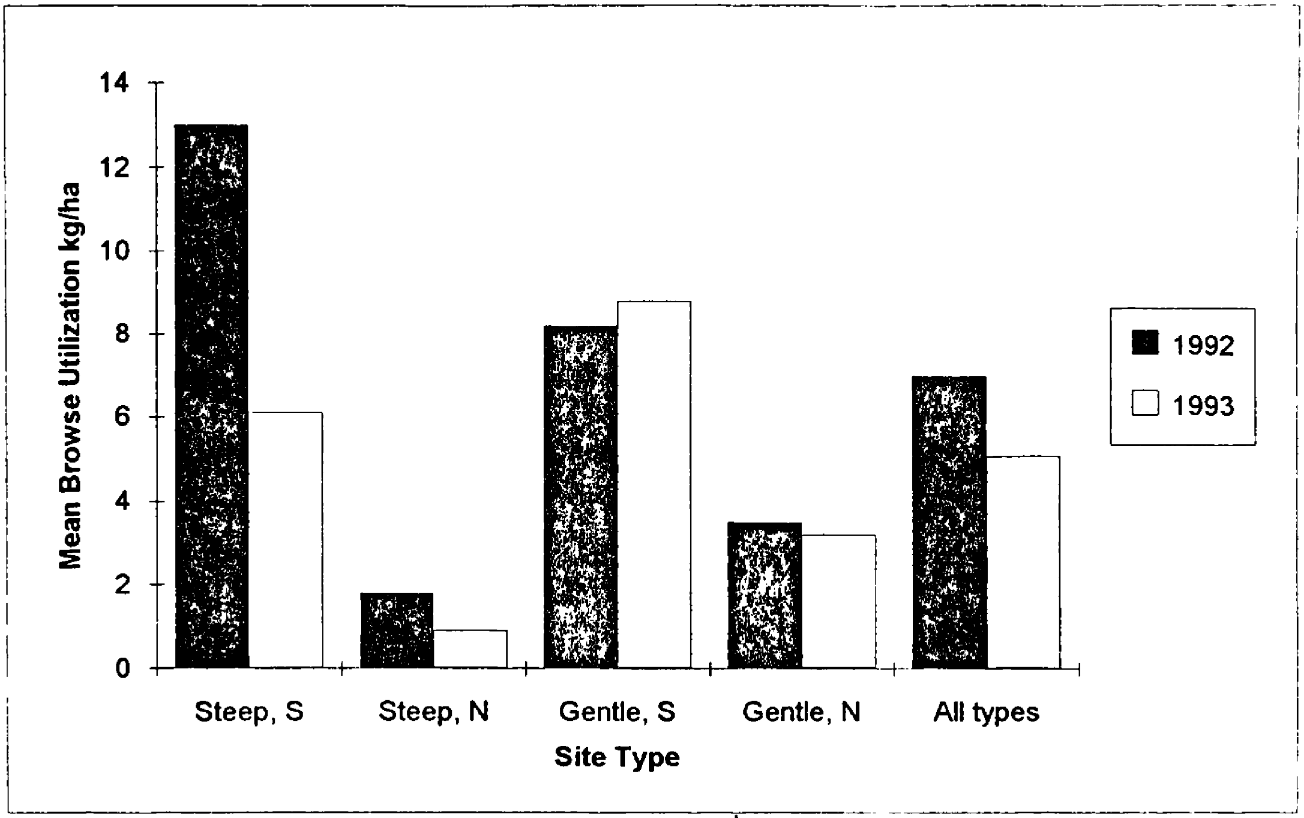


Figure 33. Current annual growth (CAG) utilization mean plot kg/ha for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Estimates were derived from CAG diameter data only. Plot data were ln transformed and means were tested for significance. No significant differences in means between years were observed ($P > 0.05$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

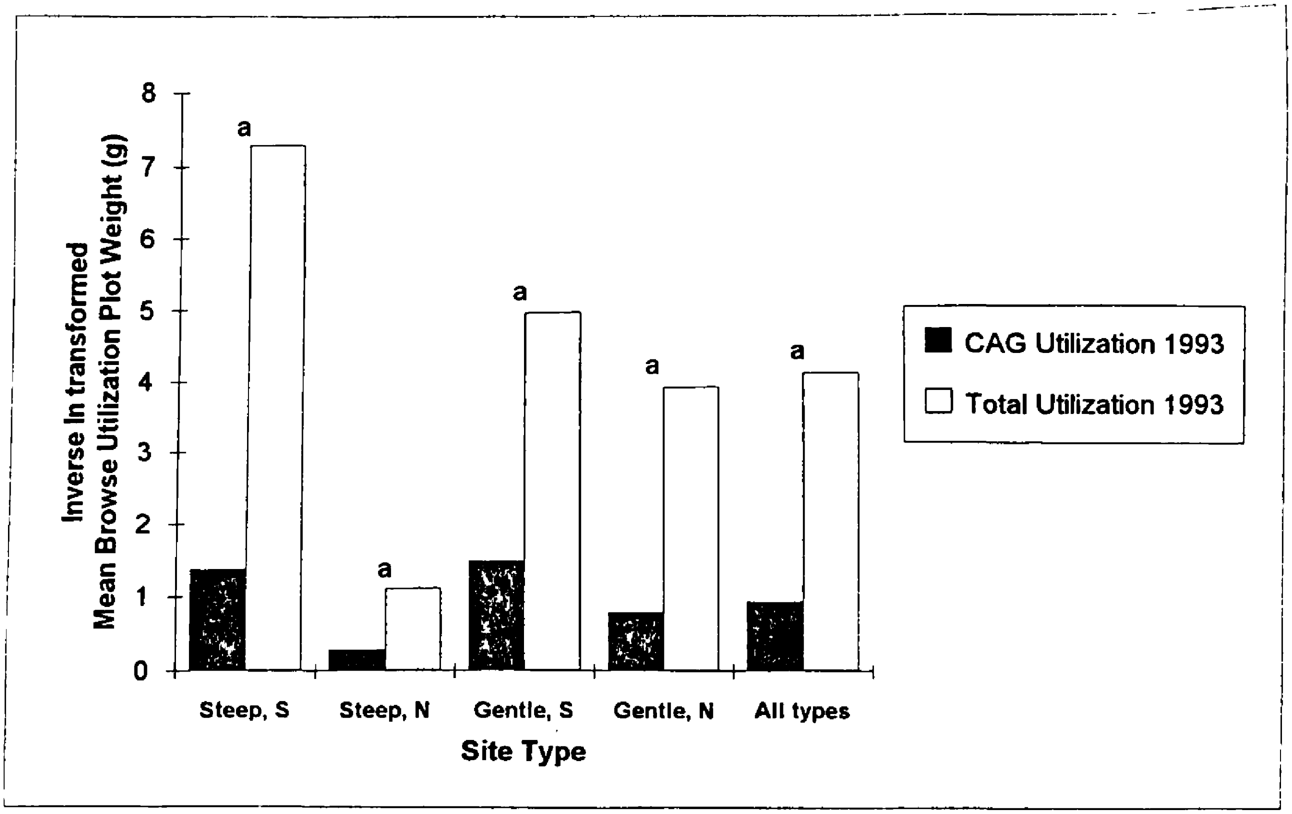


Figure 34. Comparison of current annual growth (CAG) utilization mean plot weight (g) (weight estimates from browsed CAG diameters only) and total CAG utilization (g) (CAG estimates from diameters + all unaccounted for CAG) for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Values are inverse ln means calculated from ln transformed 1993 plot data. a = significant difference in means was observed ($P < 0.001$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

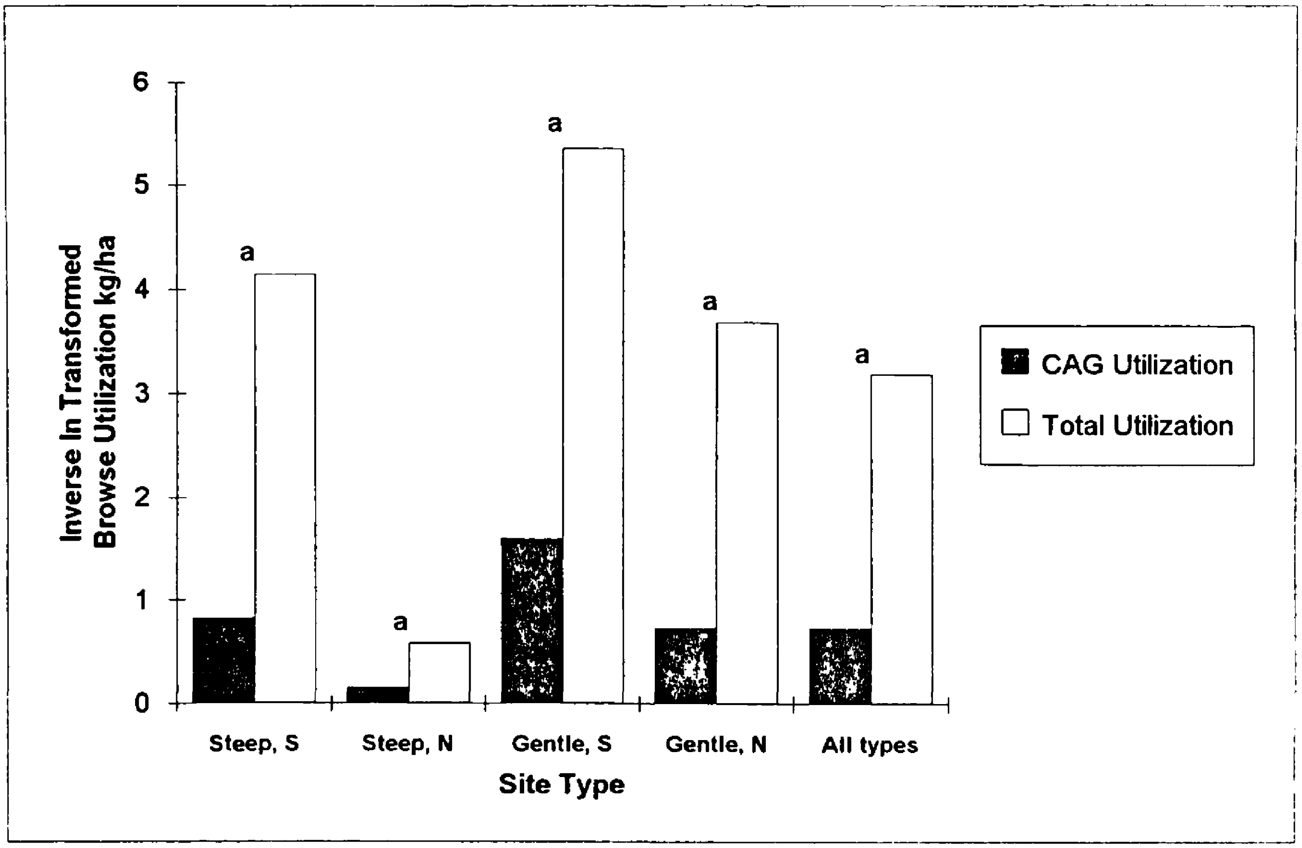


Figure 35. Comparison between browse current annual growth (CAG) utilization mean plot weights (weight estimates from browsed CAG diameters only), and total CAG utilization mean plot weight estimates (CAG estimates from diameters + unaccounted for CAG estimates) for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Kg/ha means are inverse values of ln transformed 1993 plot data. a = significant difference in means was observed ($P < 0.001$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

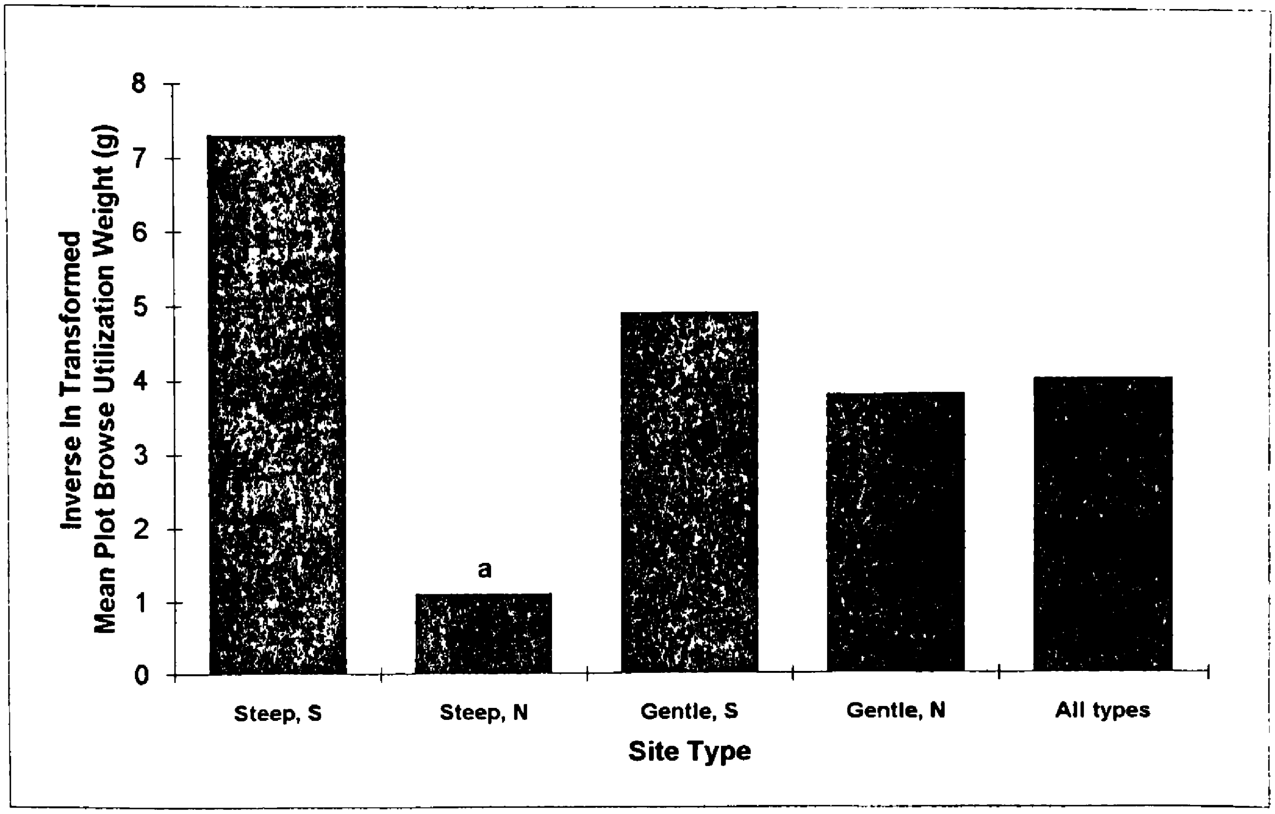


Figure 36. Total mean plot utilization weight (g) for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined for winter 1993. Values are inverse ln means calculated from ln transformed plot data. a = significantly lower mean than types Steep,S and Gentle,S ($P < 0.05$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

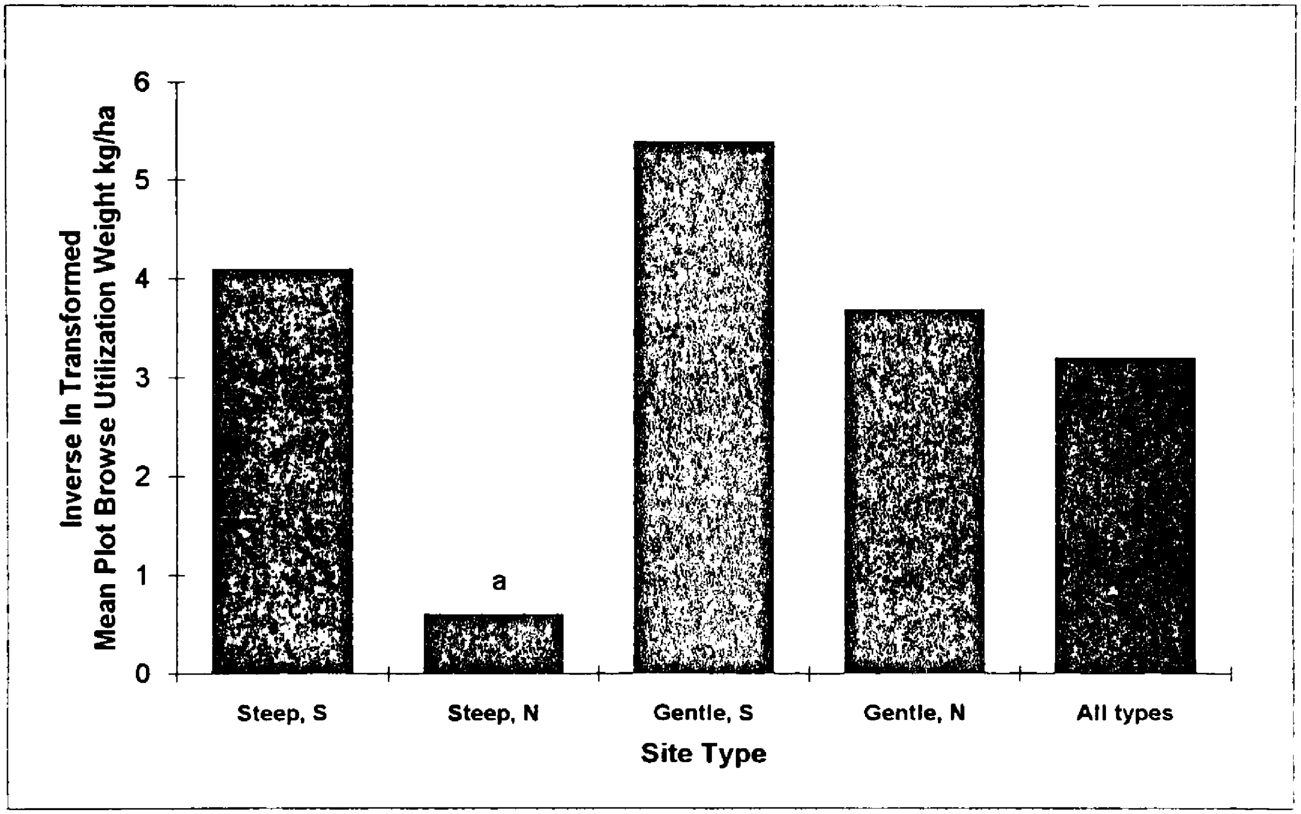


Figure 37. Total browse utilization mean plot kg/ha for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined for winter 1993. Values are inverse ln means calculated from ln transformed plot data. a = significantly lower mean than all other types ($P < 0.05$).

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

total kg/ha estimates; however, they were quite dissimilar (Table 27).

Weight utilization estimates (g) for 1993 were greatest for serviceberry. However, the percentage of production consumed in 1993 was greater for chokecherry (Table 28). The 1993 total percent weight utilization estimate for combined weight data, browse species and plots was 51.6% (Table 28). Comparison of species contributions to utilization (Table 29) with species contributions to production (Table 17) suggested that Rocky Mountain maple, chokecherry and upland willow may have been preferred browse species.

Percentages of previous year's growth stems browsed of all twigs observed browsed were greater in 1993 for all shrub species examined except chokecherry ($P < 0.05$) (Fig. 38).

Browsed diameter and unaccounted-for utilization weight estimates combined for 1993 (estimated using kg sampled/ha sampled) yielded a percentage-use range of 34-57% (Fig. 39). The greatest weight used was for the gentle-south type; however, the greatest percentage use of weight produced was for the steep-south type (Fig. 39). The lowest amount and percentage of use was observed on the steep-north type. Unaccounted-for twig weight estimates (or assumed CAG utilization) made up a substantial portion of total utilization for each site type (Fig. 39).

Table 28. Browse utilization weight (g) and percent estimates derived using browsed current annual growth diameters only (CAG Diameters), total CAG weight utilization estimates (Total), 1992 production estimates, and percent utilization estimates (% Utilization) for CAG twigs sampled on 95 plots on the BCWMA. Total and % utilization estimates were not calculated for 1992.

	1992		1993						
	CAG Diameters		CAG Diameters		*Total		Production 1992		*% Utilization
Species[a]	Weight Removed (g)	%	Weight Removed (g)	%	Weight Removed (g)	%	Weight Produced (g)	%	(Weight removed (g) / Weight produced (g)) x 100
Acgl	69.4	23.6	43.1	16.8	124.1	16.3	191.5	13.0	64.8
Amal	154.3	52.4	133.4	52.2	473.0	62.3	979.8	66.6	48.3
Ceve	17.3	5.9	31.6	12.4	73.7	9.7	146.8	10.0	50.2
Cost	15.1	5.1	21.0	8.2	37.6	4.9	88.3	6.0	42.6
Prvi	22.3	7.6	17.1	6.7	33.9	4.5	41.7	2.8	81.3
Sasc	16.0	5.4	9.4	3.7	17.3	2.3	23.9	1.6	72.4
Total	294.3	100.0	255.7	100.0	759.6	100.0	1,472.0	100.0	51.6

a = Acgl = Rocky Mountain maple, Amal = Serviceberry, Ceve = Snowbrush ceanothus, Cost = Red-osier dogwood, Prvi = Chokecherry, Sasc = Scouler willow.

* Explanitory Formulas for Total Weight Removed and % Utilization Estimates 1993.

Formulas:	Example (1993 all species sum):
A + B = C	255.6 + 712.4 = 968g
D - C = E	1,472 - 968 = 504g
E + A = F	504 + 255.6 = 759.6g
F/D x 100 = T	759.6/1,472 x 100 = 51.6%

where

A = CAG utilization weight (g) estimated from browsed diameters only (= 255.6g) (column heading "CAG Diameters").
B = Total remaining CAG weight on plot (post-winter remaining production) (= 712.4g) (column heading not listed).
C = Sum A and B (total accounted for CAG weight, post utilization) (= 968g).
D = Total 1992 browse production estimate (= 1,472g).
E = Weight estimate for unaccounted for CAG twigs browsed (represented by browsed coarse prior year's growth) (= 504g).
F = Best estimate of total weight browsed (= 759.6g) (column heading "Total").
T = Percent total weight utilization (= 51.6 %) (column heading "% Utilization").

Table 29. Current annual growth (CAG) weight percentages for 6 shrub species utilized on 4 site types during winters 1992 and 1993 on the BCWMA. Percentages reflect species' contributions to CAG browse weight utilization for each site type.

	% CAG Browse Weight Utilization[a]							
[b]	*Steep,S		*Steep,N		*Gentle,S		*Gentle,N	
Species	1992	1993	1992	1993	1992	1993	1992	1993
Acgl	28.6	14.3	43.8	46.7	10.6	5.9	24.9	31.9
Amal	39.9	35.7	53.2	50.2	70.1	71.5	52.9	50.3
Ceve	13.8	32.4	0.0	0.0	0.0	0.0	0.0	0.0
Cost	0.0	0.0	0.0	0.0	11.0	16.5	9.0	11.3
Prvi	17.7	17.6	0.0	0.0	0.0	0.0	0.0	0.0
Sasc	0.0	0.0	3.0	3.1	8.3	6.1	13.2	6.5
Sum	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

a = Percentages were derived from CAG browsed diameter weight estimates only.

b = Acgl = Rocky Mountain maple, Amal = Serviceberry, Ceve = Snowbrush ceanothus, Cost = Red-osier dogwood, Prvi = Chokecherry, Sasc = Scouler willow.

*Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.

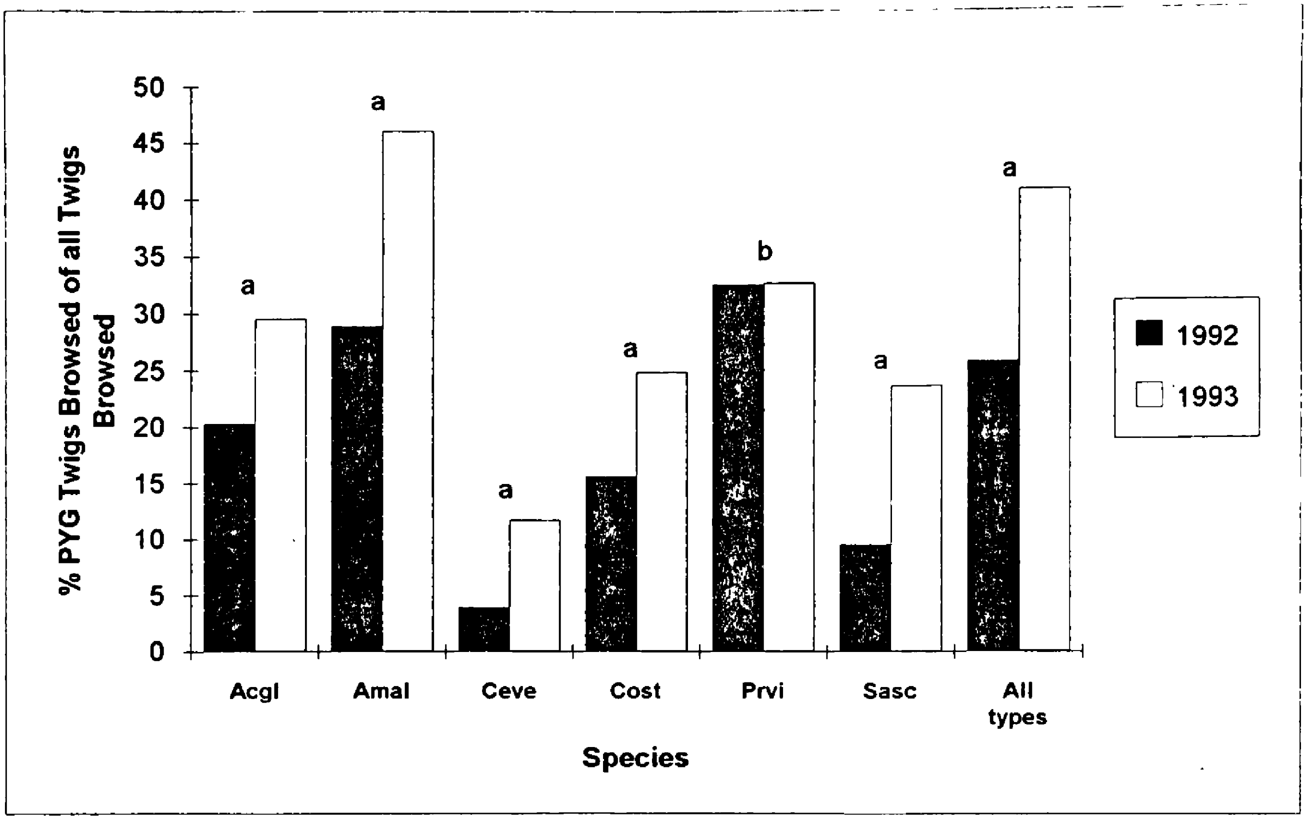


Figure 38. Percentage of coarse previous year's growth (PYG) twigs browsed of all twigs that were observed browsed during winters of 1992 and 1993 for 6 shrub species on the BCWMA. a = significant differences were observed between years ($P < 0.05$), and b = differences between years not significant ($P > 0.05$). Acgl = Rocky Mountain maple, Amal = serviceberry, Ceve = snowbrush ceanothus, Cost = red-osier dogwood, Prvi = chokecherry, Sasc = scouler willow, All types = all species combined.

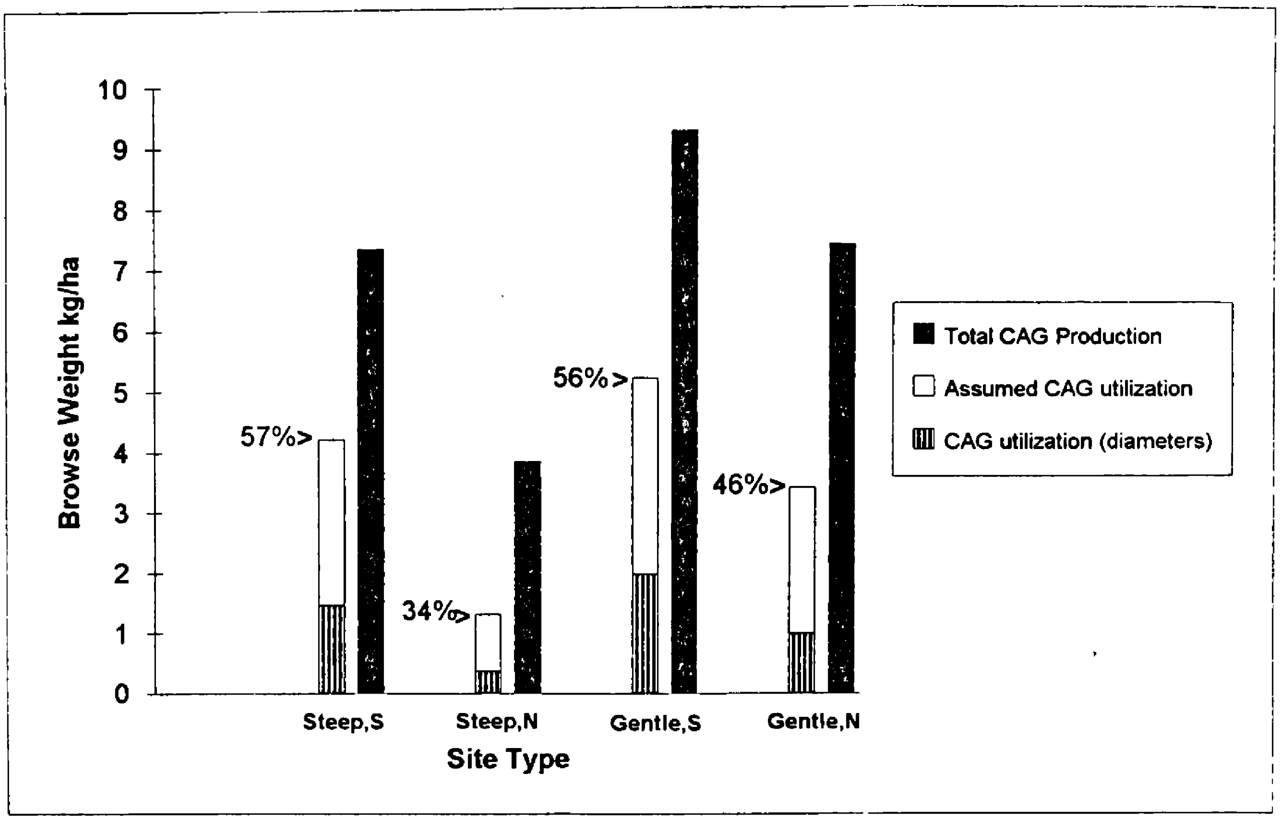


Figure 39. Browse production (sampled late summer 1992) and utilization (sampled early spring 1993) in kg/ha for ceanothus, chokecherry, red-osier dogwood, Rocky Mountain maple, serviceberry and upland willow combined. Estimates were derived using the plot weight estimate sum/total plot area sampled for each site type. Percentages are total current annual growth weight utilization estimates for 1993. Assumed CAG utilization = unaccounted-for twig estimates. CAG utilization (diameters) = estimates derived from browsed CAG diameters.

Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.

Browse Condition and Summer Utilization

The mean percentage of dead stems per plot was similar for all site types (Table 30). The steep-south type possessed the shortest shrubs; 64% of these plots were dominated by shrubs from 0-2.0 m tall (Table 30). Shrubs greater than 2.0 m tall were the most common for the other 3 types (Table 30). The mutilated form class (Cole 1957a) was most characteristic for all site types (Table 30). The steep-north type had the greatest percentage of plots with normal growth form (36%) and the steep-south type had the lowest (8%). Percentages of sprouts were greatest on steep types, but type means were all less than 4% (Table 30). Mean percentages of twigs browsed in summer were greater in 1991, and the greatest means were observed on the steep-north type during both years (Table 30).

Table 30. Browse condition results for 1991, and summer utilization for 1991 and 1992 on the BCWMA.

Browse Type[a]	Plot n	Dead stems Mean% (SD)[b]	Browse Avail. class[c]	Form Class[d]	Sprouts Mean% (SD)[e]	1991 Twigs Browsed Mean% (SD)[f]	1992 Twigs Browsed Mean% (SD)[f]
Steep,S	25	34 (13.8)	1=12% 2=52% 3=28% 4=8%	N=8% M=92%	2.9 (3.6)	14 (18.4)	8 (12.2)
Steep,N	14	32 (20.4)	2=29% 3=71%	N=36% M=57% D=7%	3.5 (12.2)	19 (22.4)	18 (19.4)
Gentle,S	25	27 (15.1)	1=4% 2=16% 3=80%	N=20% M=80%	0.4 (0.7)	14 (21.1)	9 (11.7)
Gentle,N	31	37 (19.9)	1=9% 2=10% 3=81%	N=29% M=71%	0.8 (1.4)	16 (18.0)	9 (11.6)
All types	95	33 (17.5)	1=7% 2=25% 3=65% 4=3%	N=22% M=77% D=1%	1.6 (5.1)	15 (19.4)	10 (13.4)

a = Steep,S = sites with slope >20% and southerly exposure.
Steep,N = sites with slope >20% and northerly exposure.
Gentle,S = sites with slope <20% and southerly exposure.
Gentle,N = sites with slope <20% and northerly exposure.
All types = all sites combined.

b = Mean visual estimate percentages of dead mainstems of all mainstems observed in plot vicinities.

c = Percentages of plots with:
1 = >50% of shrubs in plot vicinity 0.3-2.0 m tall ("all available").
2 = >50% of shrubs in plot vicinity <0.3 m tall ("partially available").
3 = >50% of shrubs in plot vicinity >2.0 m tall ("partially available").
4 = >50% of shrubs in plot vicinity <0.3 m or >2.0 m tall ("unavailable").
Adapted from Cole (1957a).

d = Percentage of plots with >50% of mainstems in plot vicinity:
N = Normal
M = Mutilated
D = Dead
Form classes from Cole (1957a).

e = Mean plot percentages of sprouts produced (of 100 twigs counted per plot).

f = values are summer utilization mean plot visual estimates for browsed CAG twigs. The summer utilization period of use was approximately May 15 - August 15.

DISCUSSION

The most accurate estimates for production and utilization were expected to be those weighted by plot area (i.e., kg sampled/ha sampled). The 1991 production estimate (8.72 kg/ha) was selected for the calculation of browse forage days because precipitation 7-8 months preceding sampling more closely approximated the 30-year average. Production differences observed between 1991 and 1992 estimates were likely a result of varying precipitation and growing conditions (Young and Payne 1948, Shepherd 1971). Concerns about the accuracy of the 8.72 kg/ha estimate are primarily academic, since an estimate 3 times greater leads to the same general conclusion: forage other than the 6 shrub species examined is very important to cervids wintering on the BCWMA. Although browse appeared to be abundant, it probably could not solely support wintering cervids at high densities for periods >2 weeks. Results suggested that sole browse use at 50% weight utilization could maintain cervids at current approximated population levels for about 4.5 days.

During-winter utilization estimates for percent twigs browsed and mean twig length were calculated for the 6 shrub species of interest to assess the timing and extent of browse removal. I hypothesized that if cervid populations were at or above ecological carrying capacity (Caughley

1979), browse removal would be extensive and occur early in winter. Furthermore, the occurrence of heavy shrub-use earlier than heavy conifer-use (documented in food habits results) would have supported the possibility of forage switching to presumably less palatable emergency coniferous forage (Boll 1958, Greer 1970).

There were potential biases with visual observations due to observation subjectivity (Jensen and Scotter 1977), and snow-caused differential availability of twigs among sample periods. However, several conclusions could be made from quantified observations. Above-snow unbrowsed twig percentages were not extremely limited for most segments throughout both winters (>30%), and browsed twig estimates approaching 100% were only observed on 2% of the browse segments during the mid-winter period. Further, sites where 100% of the CAG twigs showed some evidence of browsing never had 100% of their weight or length utilized. The significance of these observations is difficult to fully assess without knowledge of corresponding foraging energetics (Wickstrom et al. 1984). However, the fact remained that some unbrowsed twigs persisted above snow on most sites throughout both winters.

In January 1993, heavy use of conifers and light use of browse by MD and WTD, concurrent with non-restrictive snow conditions and substantial browse abundance and availability, suggested a possible forage preference for conifers over browse. Substantial non-emergency use of Douglas-fir and ponderosa pine as winter forage by MD or WTD has been documented in other studies (Morris and Schwartz 1957, Kufeld et al. 1973, Crouch 1981, Peek 1984, Jenkins 1985, Seeley 1985, Pac et al. 1991).

During winter, visual utilization estimates also indicated that substantial browse-use occurred earlier than January in 1992 and then declined, whereas use likely peaked in late January or early February 1993 and was more constant over the entire winter. Seemingly impossible decreased percentages of twigs browsed and greater twig lengths observed in March were a result of increased browse availability as snow melted.

Clipping studies by Young and Payne (1948) and Shepherd (1971) indicated that serviceberry was highly tolerant of clipping. Young and Payne (1948) observed that shrubs clipped from 5 June to 15 September could withstand continual CAG length reductions of 60-65%, and that production varied with seasonal clipping. Similar observations made by Shepherd (1971) indicated that mid to late summer clipping levels of up to 60% annually, enhanced production of serviceberry plants, but that sustained use of 80% or more decreased subsequent production yields. Shepherd (1971) also observed that destructive clipping of serviceberry beyond CAG stimulated sprouting and increased production, but resulted in substantially decreased weight yields after 4 years.

The combined post-winter percent utilization weight estimate for the 6 shrub species in 1993 (51.6%) suggested that most shrubs were being utilized at levels below 60% during a relatively difficult winter. Further, serviceberry weight utilization (48.3%) was well below destructive levels of 80% indicated by Shepherd (1971). However, significant differences were observed in mean percent utilization by browse type, and individual shrubs growing in high-use areas on the BCWMA were occasionally subject to substantial use beyond CAG. In general, observations of serviceberry made on the BCWMA also indicated its strong tolerance of CAG removal.

Several studies have shown that many shrub species can tolerate fall browsing levels of 50-80%, and fall utilization of up to 60% year after year has been considered acceptable (Young and Payne 1948, Krefting et al. 1966, Shepherd 1971, Anderson et al. 1972). Although seasonal and geographic differences would be expected, a proper use rule of thumb value of < 60% winter utilization is probably not unreasonable for similar shrub species growing in comparable environments. Shrub species most likely to suffer adverse effects as a result of overuse on the BCWMA (based on 60% proper use) were chokecherry, upland willow and Rocky Mountain maple.

Removal of CAG early in the growing season appeared to be considerably more destructive than winter browsing. I observed that the removal of apical buds, or leaves stripped from developing CAG shoots, frequently resulted in desiccation and death of 50-100% of the remaining stem. Severe influences of spring browsing were also reported by Young and Payne (1948).

Stickney (1966) observed that approximately 60% length utilization occurred on serviceberry when about 100% of available twigs were browsed. In contrast, this study documented 48% weight utilization of serviceberry when about 36% of the available twigs were browsed. Differences in findings may be attributed to weight vs. length utilization comparisons, or behavioral differences in substantial browsing by deer (Stickney 1966) vs. more severe browsing by elk in this study. Similarly, Peek et al. (1971) observed that moose generally browsed twigs to a larger diameter than WTD in northern Minnesota. Fuller (1976) observed that the percent-twigs-browsed method underestimated utilization by elk on serviceberry and Rocky Mountain maple on the Spotted Bear Mountain winter range. The BCWMA study may also have examined browse on more sites with marginal winter habitat characteristics and greater extremes of browse use than sites examined by Stickney (1966). One or more of these factors might have altered number-browsed and weight-removed percentages for browsed twigs.

Browse research has primarily considered production and utilization of CAG, since CAG is normally the most nutritious portion of palatable shrubs (Cole 1957a, Stickney 1966, Lyon 1970, Fuller 1976, Jensen and Scotter 1977, Makela 1990, Pitt and Schwab 1990). However, Fuller (1976) documented elk-use of serviceberry and Rocky Mountain maple twigs beyond CAG when length utilization was generally < 60%. I also frequently observed the use of stems beyond CAG on shrubs where abundant unbrowsed CAG remained. This occurred in areas frequented by deer and elk, and indicated that cervids were not as selective for CAG as previously believed. Moreover, estimates that considered only CAG browsed stems, and ignored CAG removed from browsed PYG stems, potentially underestimated utilization by a 3-fold margin.

Other factors may have influenced high observed levels of PYG utilization where CAG was also present. Some PYG browsed stems without measurable CAG may have had abundant buds that were obtained through PYG utilization by elk or deer. Other PYG stems appeared browsed, but may have been inadvertently broken while foraging on CAG. Observer error in confusing CAG with PYG was possible; however, continual comparisons of differences in stem characteristics on each shrub were made and should have minimized this error. Stems that reflected cervid browsing beyond CAG were usually obvious.

Several studies have placed lower emphasis on browse growing at heights below 0.3 m (Cole 1957a, Asherin 1976). However, results from this study suggested that browse at this height received substantial use during mild and normal winters on the BCWMA. Browse growing at this level would not provide emergency winter forage during periods with deep snow, but most winters are likely to have periodic conditions that would favor browsing at low heights. Therefore, its importance during most winters may be underestimated.

Results of the general condition of browse plants were difficult to interpret. Mean percent dead stems was a poor indicator of productivity because some sites had low apparent productivity and few dead stems. Shrubs on recently burned sites were generally productive with cages of abundant dead stems. Previous treatment intensity, time and type were all expected to influence standing dead stems. Dead stem counts as an index for shrub productivity should be taken after sites are previously cleared of all dead stems (Shepherd 1971). After clearing, Shepherd (1971) observed an accumulation of < 50% dead stems for shrubs destructively clipped beyond CAG for 7 years, while shrubs with 100% CAG removed for 10 years accumulated < 20% dead stems. Natural accumulations of dead stems on the BCWMA of 30% were common, but they rarely exceeded 50%.

The mutilated growth form of stems probably reflected their relatively old ages as well as browsing in previous years (Lonner 1972). The abundance of mutilated stems and relatively low percentages of browse in diets implied that less visually obvious utilization effects on other forage items may have been substantial.

Mean percentages of CAG stems that were sprouts (1.6%) approximated those observed by Shepherd (1971) on unclipped control shrubs (1.9%). Shrubs in the Shepherd (1971) study that received 100% and destructive clip treatments had 7.1% and 11.1% sprouts respectively.

Observed inconsistencies in comparable mean plot weight (kg/ha) and kg sampled/ha sampled estimates for production and utilization indicated that mean plot weight was a relatively inaccurate estimator for production and utilization. Specifically, mean plot kg/ha estimates were consistently high because (by definition) short plots always contributed high weight estimates, and long plots always contributed low weight estimates. When averaged, short plots exaggerated mean plot weights. Variance estimates were also exaggerated because they reflected variation of shrubs sampled on plots and variation in plot lengths.

Although ln transformations effectively normalized kg/ha data sets, the transformation influence on ratio estimates may provide unreliable results when tested (A. Sheldon, Univ. Mont., pers. commun.). Suggested methods for future browse research would incorporate plots of fixed size and number per type.

CHAPTER 4: SYNTHESIS

For the past 15 years the BCWMA has been managed for the maximum sustainable utilization of the winter range by elk, MD and WTD populations (BCWMA Draft Rev. Manage. Plan, MDFWP, Missoula, 1989). This management strategy, combined with frequent mild winters, promoted high elk, MD and WTD densities observed during this study. The sustainability of high cervid densities on the BCWMA was of concern to managers because the potential for interspecific competition was expected to increase as a result of intensified interaction (Wydeven and Dahlgren 1985), and reduced forage availability from cumulative utilization (Greer 1970, Sinclair 1977, Houston 1982). Substantial interspecific competition for browse was expected to result in significantly reduced numbers in one or more of the closely related populations over time (Hardin 1960, Houston 1982). Therefore, quantitative assessments of potential competitive interactions and browse use were desired.

Many studies have relied upon inference-based methodologies to evaluate interspecific competition among free-ranging herbivores (Constan 1972, Kramer 1973, Hansen and Reid 1975, Anthony and Smith 1977, Dunbar 1978, Leuthold 1978, Singer 1979, Schwartz and Ellis 1981, Wydeven and Dahlgren 1985, Jenkins and Wright 1988, this study). Studies that clearly distinguish interspecific competition utilize controlled experiments that measure niche responses to manipulations of abundances of one or more hypothetically competing species (Connell 1980, Schoener 1983). While such experiments are practical using plants or small short-lived species in laboratories (Schoener 1983), influences of environmental variability and resource availability on wild ungulate populations are difficult to control (Jenkins 1985). Further, sufficient perturbations of free-ranging ungulate populations for experimentation (Macnab 1983) can be socially unacceptable.

Weaknesses in using niche overlap to infer competition have been pointed out by several authors (Colwell and Futuyma 1971, Wiens and Rottenberry 1979, Connell 1980, Schoener 1983). Primary difficulties arise in the way observations can be interpreted, and in obtaining accurate assessments of resource availability. High overlap when resources are limited may indicate competition (Jenkins and Wright 1988), tolerance (Colwell and Futuyma 1971, Sinclair 1977:81, Schoener 1983), commensalism (Baty et al. 1993) or optimization (e.g., utilization of different parts of the same plant species, or consuming the same plants that are dispersed differently; Bell 1971, Sinclair 1977:273). High overlap when resources are not limiting is common, because preferences by species for the same resources are not limited by resource availability (Wiens and Rottenberry 1979, Schoener 1982). Low overlap when resources are abundant intuitively signifies little competitive interaction, whereas low overlap when resources are limiting can indicate reduced interspecific competition through increased partitioning (Schoener 1982) or increased competition through aggressive exclusion (Schoener 1983). The significance of overlap indices are also often theoretical and have no proven biological basis (Connell 1980). Consequently, firm conclusions about competition drawn from niche overlap studies should be carefully considered.

Several authors have made inferences about competition by comparing niche overlap between periods with different resource availabilities (Anthony and Smith 1977, Dunbar 1978, Leuthold 1978, Jenkins and Wright 1988). High niche overlap during periods of low resource availability has been considered evidence for competition (Anthony and Smith 1977, Singer 1979, Jenkins and Wright 1988), while reduced overlap has provided evidence for coevolutionary divergence (Hardin 1960, Schoener 1982).

This study was designed to evaluate and document resource-use overlap within and between two winters on a study area where winter ecology of sympatric cervids had not been studied. Although niche overlap evaluation alone has limited ability to reveal interspecific competition, estimates of resource-use overlap, mortality and recruitment under naturally changing resource availabilities during this study were expected to provide insights into the ecology of wintering cervids, especially when compared with the results of Jenkins (1985) and Jenkins and Wright (1988). It was not an objective, nor was it possible, to evaluate the extent of actual interspecific competition on the BCWMA.

Initial hypotheses of this study were: (1) substantial spatial and habitat overlap among the three species occurred in winter, especially when elk moved into forested habitats as snow conditions worsened (M. A. Hurley, Univ. Idaho, pers. commun.); (2) substantial dietary overlap was expected in forested habitats, and deciduous browse was expected to be a primary limiting resource (M. A. Hurley, Univ. Idaho, pers. commun.; Wallmo and Regelin 1981; Nelson and Leege 1982; Peek 1984); and (3) elk were expected to be dominant competitors (Mackie 1970, Jenkins 1985) due to lower forage quality requirements (Hobbs et al. 1983), ability to tolerate deep snow (Houston 1982, Jenkins 1985) and greater foraging height (Jenkins and Wright 1988); and (4) reduced recruitment and substantial over-winter mortality in one or more of the cervid populations, and high resource overlap during periods of low forage availability would provide further evidence for intense interspecific competition (Houston 1982, Jenkins and Wright 1988).

Overlap indices for 1993 were used to make inferences about habitat and spatial overlap relative to snow depth because 1993 data were less influenced by the October 1991 wildfire. While 1993 overlap indices indicated that habitat overlap increased between elk and MD during a period with greater mean snow depths (February 1993), spatial overlap decreased slightly.

Habitat and spatial overlap between elk and MD was relatively high in each of the four time periods examined, which supported hypothesis 1. Greater overlap within spatial zones occurred between elk and both deer species when snow was deepest on rough fescue grasslands. Seventy-six percent of elk tracks recorded in 1993 on rough fescue grasslands were counted when snow depths there were shallowest.

Grass forage burned by the October 1991 wildfire partially simulated reduced forage availability that might normally result from deep snow (Jenkins and Wright 1987, Schwab et al. 1987). Reduced grass availability caused by fire-removal was the likely influence that caused approximately 60% of the normal wintering elk herd to disperse to adjacent unburned habitats in early winter 1992. Reduced grass availability for elk was also the likely cause for greater spatial, habitat and dietary overlap indices obtained for elk-MD and elk-WTD species pairs in 1992.

Habitat overlap between MD and WTD was relatively high during both winters due in part to affinities of both species for forested habitats. However, greater habitat and spatial overlap between MD and WTD in 1992 was not observed, indicating that interspecific interactions between them were not greatly influenced by the removal of grass forage. Graminoid estimates never exceeded 18% for any observed MD or WTD diet during January or February of both years. With the exception of January 1993 results, spatial overlap was substantially lower between MD and WTD than for elk-MD or elk-WTD pairs. Moreover, spatial overlap among MD and WTD was extremely low (0.09) when snow was deepest during this study (in February 1993).

The extent of habitat and spatial overlap between elk and WTD was consistently lower than for elk and MD during both winters. Factors that may have influenced this were: (1) WTD concentrated in a narrowly defined spatial zone that was bordered by a highway with considerable vehicular traffic (zone 1, Fig. 12, Chapter 2), (2) grasslands preferred by elk were less accessible from zone 1, (3) browse was sparse in zone 1, and (4) the abundance of other preferred forage types may have been reduced by persistent WTD wintering at high densities. In this instance zone 1 may have functioned for WTD as a sparse foraging area that served as an ecological refuge from elk (Sinclair 1977:272, Houston 1982:183, Jenkins and Wright 1988).

Relatively common sightings of small elk groups of 5-20 individuals in close proximity (20-30 m) to WTD groups of 3-10 individuals suggested that direct WTD displacement of elk was unlikely or minimal. Moreover, a possible commensal relationship that benefitted WTD during periods with deep snow was noted (Baty et al. 1993), which paralleled African ungulate-forage relationships observed by Bell (1971).

Substantial dietary overlap was not observed between elk-MD and elk-WTD species pairs during this study. However, dietary overlap indices were greater between elk-MD and elk-WTD species pairs when bunchgrass availability was limited in 1992. Diet overlap for elk-MD and elk-WTD pairs was lower in 1993 when snow was deeper, which indicated that bunchgrass removal by the 1991 wildfire had a greater influence on forage availability for elk than did deeper snow. Diet overlap in 1993 was greater between elk-MD and elk-WTD species pairs in February, which was presumably the time when nutritional constraints were more limiting during that year. However, these diet overlap indices were still relatively low.

Diet overlap indices appeared to be independent of changes in habitat overlap. Diets were likely influenced by differential forage preferences of elk, MD and WTD using similar habitats (Hobbs et al. 1983). Although grass forage availability was substantially reduced in 1992, elk maintained diets high in graminoids while foraging in forested habitats by consuming high quantities of elk sedge (Appendices D and E). Deeper snow that would further limit low-growing forage types in forested habitats would be expected to increase dietary overlap among elk, MD and WTD

(Jenkins 1985).

Substantial dietary overlap between MD and WTD was observed throughout both winters. However, dietary overlap slightly decreased during February 1993 (i.e., the more nutritionally limited month in 1993). Reduced dietary overlap between MD and WTD during this period primarily resulted from a shift in WTD diets. WTD decreased their use of serviceberry (due in part to lower availability caused by prior consumption) and increased their use of tree lichens and bearberry. MD and WTD diet similarity during both winters resulted from common use of Douglas-fir, Oregon grape, ponderosa pine, and serviceberry (Appendices D and E). These forage species were abundant and wide spread on the study area; however, food habits results indicated that Oregon grape was used less when snow was deep.

Jenkins (1985) observed substantial use of deciduous browse by elk (36-46%) and WTD (22-40%) during 2 consecutive winters in the North Fork of the Flathead River Basin. However, deciduous browse was not used as extensively during 2 consecutive winters by elk, MD or WTD on the BCWMA (all cervids 3-20%). Graminoids were consistently consumed by elk in greater amounts than any other forage class (60-82%) on the BCWMA, whereas MD and WTD consumed greater amounts of coniferous browse (43-74%). Similar to WTD in Jenkins' study, MD and WTD appeared to have a high preference for evergreen shrubs when available (primarily Oregon grape).

Jenkins (1985) also observed heavy use of conifers by WTD (49-51%) during both winters in the North Fork, whereas elk made greatest use of conifers (30-36%) and deciduous browse. More substantial use of graminoids by elk on the BCWMA indicated that forage resource breadth was potentially greater there. Extensive grasslands, more pronounced topographic relief and lower snow depths on the BCWMA may have increased forage availability overall, thus favoring spatial, habitat and dietary partitioning among elk, MD and WTD.

Mackie (1970:72) suggested that elk were more efficient competitors than MD in eastern Montana because they used more habitat types, topographic sites and forage classes. Jenkins (1985:125) hypothesized that elk were dominant competitors over moose and WTD in northwest Montana because they possessed broad generalist habits. Observations made during this study generally support a similar conclusion for the BCWMA. However, adaptive mechanisms were evident that enhanced MD and WTD survival on the BCWMA.

Elk on the BCWMA used larger areas comprised of more habitats, and presumably could utilize more forage types than MD and WTD (Mackie 1970, Wickstrom et al. 1984); however, graminoids were normally preferred. Elk consumed large amounts of fibrous bunchgrass that was less available to MD and WTD due to extensive snow cover (Telfer and Kelsall 1984), and was presumably less palatable (Hanley

1982, Hanley and Hanley 1982, Hobbs et al. 1983, Jenkins 1985). Observations of elk feeding in forest-browse habitats on the BCWMA indicated that elk had a greater vertical range of forage available to them because of their greater foraging height (Nelson 1982). Moreover, qualitative and quantitative observations indicated that elk groups comprised of several hundred animals could rapidly (and fairly completely) consume available browse resources.

Elk activity appeared less influenced by deep snow than for deer (Jenkins 1985, Parker et al. 1984). Telfer and Kelsall (1984) rated elk as poorly adapted behaviorally to use trail networks in preferred habitats. Conversely, elk on the BCWMA made extensive use of trails within and between preferred habitats. Beall (1974) observed that elk favored areas with snow depths < 46 cm. Frequent use of sites by elk on the BCWMA with snow depths > 46 cm may have been influenced by larger group sizes on the BCWMA, and reduced energy expenditures of individuals using trails. My observations were consistent with those of Geist (1982), who suggested that single file travel greatly reduces energy expenditure when snow is deep. However, qualitative observations also indicated that smaller group sizes of less than 20 elk were more common as they became increasingly dependent upon forested winter habitats, effectively reducing the frequency and potential benefits of trailing.

Elk are probably better adapted to withstand colder temperatures than deer (Geist 1982). Beall (1974:153) observed maximum movement by elk during periods of extremely cold clear weather. However, WTD may be forced to conserve energy under such conditions by limiting movement and seeking cover (Moen 1976). Beall (1974:153) also observed that when temperatures were between -18 to 2° C elk bedded on open slopes near feeding sites instead of areas that offered protection from the cold. The greater tendency for elk observed in this study to use non-forested habitats during cold temperature extremes provided evidence that elk tolerated lower temperatures than WTD or MD. Their ability to tolerate colder temperatures is likely influenced by their lower surface to mass ratio and thicker coat (Geist 1982).

These observations by themselves demonstrate that elk have strong competitive advantages in winter. However, observations made during this study and by other authors indicate that adaptations of MD and WTD for winter survival may allow them to remain competitive with elk in many situations. For example, MD and WTD on the BCWMA also made substantial use of trails (made by elk and deer), which reduced sinking depth and energy expenditures in deep snow (Parker et al. 1984). Although elk have greater chest heights than deer, MD and WTD have lower foot loading characteristics than elk, which minimize sinking depth in dense snow (Telfer and Kelsall 1979, Houston 1982, Parker et al. 1984). MD also tend to have proportionately longer legs than elk of similar age (Parker et al. 1984). Pengelly (1954:49) reported that distinct habitat preferences and observed interspecific tolerance promoted coexistence among elk, MD and WTD in northern Idaho.

MD and WTD may also be better adapted to compensate for substantial winter mortality because of their greater reproductive capacity than elk (Connolly 1981, Taber et al. 1982, Verme and Ullrey 1984). This would enhance their ability to inhabit cold environments with deep snow.

Morphological and physiological adaptations allow elk to consume large quantities of fibrous forage (Sinclair 1977:272, Houston 1982:175, Hobbs et al. 1983, Wickstrom et al. 1984, Jenkins 1985). However, MD and WTD have a lower absolute forage requirement (Hanley 1982), and would presumably derive greater benefit from "crumbs" left by elk than larger herbivores would (Jarman and Sinclair 1979, as referenced by Houston 1982:183). Further, MD and WTD made the greatest use of Douglas-fir, which was wide-spread, abundant and available on the BCWMA. Douglas-fir typically is high in lignin and bactericidal compounds that can inhibit digestion (Helwig 1957, Nagy et al. 1964, Gill 1972, Jenkins 1985). However, the abilities of MD and WTD on the BCWMA to subsist on relatively large amounts of conifer may have been positively influenced by increased digestibility of Douglas-fir when mixed with other forages (McCullough

1955, Dietz et al. 1962, Nagy et al. 1969, Gill 1972), faster forage processing through rapid excretion rather than rapid digestion (Hanley 1982, Hobbs et al. 1983), and high palatability of the Douglas-fir genotype (Dimock et al. 1976, Radwan 1972) found on the BCWMA.

MD and WTD also possess individual adaptations that would further increase their ability to coexist. On the BCWMA, MD frequented sites with deeper and more crusted snow than WTD. Moreover, sites used by MD generally had greater accumulations of snow than sites used by elk. MD are also adept at collapsing the phalanx to increase their foot area, which reduces foot loading and facilitates locomotion in deep snow (Parker et al. 1984). MD on the BCWMA also used colder habitats, were less restricted to habitats with dense overstory cover, and maintained a broader spatial distribution than WTD. Although MD and WTD diets were very similar, the broad spatial distribution of MD reduced the potential for competition through utilization of identical foods dispersed differently (Sinclair 1977:273). In addition, broad spatial distribution of prey into complex predator-free environments may have functioned to reduce predation on MD (Ricklefs 1979:593,601).

WTD on the BCWMA exhibited a greater tendency to conserve energy through habitat selection than MD or elk (Moen 1976). Yarding behavior of WTD increased energy conservation (Moen 1976, Potvin and Huot 1983, Telfer and

Kelsall 1984), and may have decreased losses to predation through trail networks and environmental familiarization (Nelson and Mech 1981). Finally, WTD not only appeared to take advantage of an ecological refuge from MD and elk (Sinclair 1977:272, Houston 1982:183, Jenkins and Wright 1988), but also potentially created it.

Creation of an ecological refuge in this instance may have occurred through "preemptive competition" (Schoener 1983:257), which occurs when a unit of space is passively occupied by an individual, thereby causing other individuals not to occupy that space before the occupant leaves. WTD on the BCWMA shifted abruptly to preferred habitats early, and persisted at high densities, in apparent response to deepening snow. Because interspecific aggressive behavior was never observed (Baty et al. 1993), a logical hypothesis was that WTD at high densities passively deterred use of spatial zone 1 by MD. This may have been accomplished through the visual and olfactory presence of numerous WTD. Aggressive defense of feeding territories in deep snow environments would impose substantial costs on individuals exhibiting such behavior (Parker et al. 1984). Therefore, because of restricted mobility and reduced forage availability influenced by deep snow, aggressive interspecific behavior among cervids would be of little advantage (Geist 1982). Suspected factors contributing to the passive creation of a WTD refuge were that MD were less dependent upon habitats with dense overstory canopy, and they were less responsive in early winter to moderately deep snow conditions.

One hypothesis with regard to a dominant winter competitor is that one species is not necessarily better adapted to deep snow than another (Parker et al. 1984). Rather, each species possesses selective advantages that benefit their populations under a variety of environmental conditions (Geist 1982). This can be observed by considering the abilities of elk, MD and WTD to succeed in environments where severe winters are common, and in their ability to coexist within a large northerly geographic region (Walmo 1981, Bryant and Maser 1982, Baker 1984, Telfer and Kelsall 1984).

Estimates for recruitment and mortality made during this study did not indicate that the elk, MD or WTD populations were suffering from severe environmental limitations when compared with other local studies. Three-year recruitment means for elk, MD and WTD on the BCWMA were slightly above regional means estimated in a similar manner, and natural mortality estimates were also low when compared with results of comparable studies (Baremore 1980 as cited by Houston 1982:57, Wood et al. 1989, Pac et al. 1991). Greater observed WTD carcass density in 1993 was presumed to be coincidental. Several WTD carcasses observed during mortality surveys were in one location and had apparently been killed by a mountain lion. This probably clumped carcass distribution, and resulted in an inflated WTD mortality estimate. Overall, above average recruitment and low observed mortality levels did little to implicate interspecific competition as limiting the elk, MD or WTD populations on the BCWMA during this study.

Interspecific Competition in Shaping Niche Relationships

Jenkins and Wright (1988) concluded that resource overlap patterns among moose, elk and WTD in the North Fork of the Flathead River Basin provided little evidence that niche relationships were shaped as a result of interspecific competition. They observed that: (1) trophic and ecological overlap did not diminish during a nutritionally limited period, and subsequently reduce interspecific competition; (2) similar-sized species possessing similar ecological requirements did not differ in resource-use traits more than species of dissimilar body size; and (3) species pairs with the greatest amount of trophic overlap did not exhibit compensatory spatial separation. Results obtained in a similar manner for elk, MD and WTD on the BCWMA supported different conclusions.

In order to address the conclusions of Jenkins and Wright (1988), it was necessary to determine the months that were most limiting nutritionally. It was assumed that Februarys of both winters were the most nutritionally limited months sampled. This assumption was based upon the qualitative assessment of food habits results, distributional polygon sizes, snow conditions, forage removal patterns and observations of increased proportions of individuals appearing in poor condition in February of both years. Assessment of nutritionally limited conditions across years was not attempted due to gross differential influences of forage availability brought about by the 1991 wildfire and transient snow conditions.

In contrast with the conclusions of Jenkins and Wright (1988), a decline in ecological overlap was observed on the BCWMA as forage availability decreased. Although decreases in overlap were relatively small and inconsistent across species pairs, it is important to consider that substantial increases in overlap during more nutritionally limited periods were not observed. Ecological overlap for all cervid pairs during all months examined was relatively low when compared with the results of Jenkins and Wright (1988), indicating a reduced potential for interspecific competition on the BCWMA.

Although similar-sized species (MD and WTD) did not consistently diverge in all resource-use traits more than species of dissimilar body size (elk and WTD), the MD-WTD species pair consistently exhibited substantial spatial separation. The MD-WTD species pair also maintained the greatest trophic overlap of all species pairs during all months, and expectedly benefitted the most from compensatory spatial separation (Hardin 1960). Further, the MD-WTD pair decreased diet, habitat and spatial overlap from January to February 1993 when foraging conditions were clearly more limiting.

Although detrimental population influences caused by interspecific competition could not be identified during this study, these results supported the three hypotheses of Jenkins and Wright (1988). This suggested that interspecific competition may have functioned in shaping niche relationships on the BCWMA.

Several differences between this study and the North Fork study potentially contributed to contradictory conclusions. Greater cervid densities on the BCWMA may have placed greater pressure on cervids to partition resources and diverge in resource-use traits. Secondly, elk, MD and WTD species pairs were generally more morphologically and trophically similar than moose, elk and WTD pairs studied in the North Fork. Finally, greater preferred forage availability, influenced by greater topographic diversity, widespread forage abundance and lower snow depths across the landscape of the BCWMA may have allowed greater expression of resource partitioning. Jenkins (1985:119) recognized partitioning limitations for areas with deep snow, and suggested that many resources simply were not available to permit greater resource partitioning during restrictive winters.

Therefore, conditions that favor greater resource availability, similar to those on the BCWMA, may facilitate substantial partitioning. Snow conditions in the North Fork of the Flathead River Basin may often be so confining that partitioning capabilities of cervids cannot be expressed (Jenkins 1985), or are not apparent using the methods incorporated during these 2 studies. In instances where resources are extremely limited, additional adaptive modifications such as partitioning of plant parts (Bell 1971), feeding on "crumbs" left by others (Jarman and Sinclair 1979), commensalism (Baty et al. 1993) and efficient energy conservation strategies (Moen 1976) may expand cervid niches, and further minimize competitive interactions.

Management Implications

When interspecific competition is identified, it is important to carefully consider the causes and consequences of the observed interactions. Houston (1982:184) considered that in many cases interspecific competition may have ecological importance, but may not indicate cause for alarm or corrective management. However, high ungulate population levels and heavily influenced plant communities normally associated with ecological carrying capacity (Caughley 1979) may have little public acceptance. Therefore, managers may be pressured to maintain sympatric elk and deer numbers at a lower economic carrying capacity where animal starvation and animal influences on plant communities are reduced (Caughley 1979).

Results from this study indicated that severe inhibition of one cervid population by another (under observed cervid densities) was unlikely under normal winter conditions. Moreover, it appeared unlikely that the removal of one cervid species would have substantially increased forage availability for another (Smith and Julander 1953), and the possibility of elk increasing forage availability for MD and WTD was recognized (Baty et al. 1993). Forage and habitat options for MD might have increased slightly in the absence of WTD; however, WTD may have used occupied habitats more efficiently and thus, maximized total deer biomass.

Intraspecific competition may have been substantial at times. Intraspecific competition was evidenced by strong affinities of each species for geographic areas used in previous years, and distinctly high-lined vegetation within such areas. High-lined vegetation apparently resulted from densely congregated cervid groups that returned year after year to the same locations. Though locally abundant, high-lined conifers were not wide spread. Future estimates of how close elk and deer populations are to ecological carrying capacity might be improved by monitoring high-lining across a winter range, as opposed to viewing localized high-lining in cervid concentration areas as evidence for starvation. Monitoring use of young conifers (especially Douglas-fir) may be of considerable importance for maintaining appropriate winter MD and WTD densities.

Specific examples of localized conifer high-lining by WTD were observed along Salmon Lake and Highway 83. Similar use by WTD has apparently occurred for many years (Janke 1977, Slott 1980). High-lining that resulted from concentrated MD use occurred primarily near Sperry Grade, and examples for elk were observed in forested stands adjacent to Blanchard Flats. Substantial utilization of rough fescue across the study area following most winters (personal observation, and M. J. Thompson, MDFWP, pers. commun.) indicated that elk densities were approaching upper limits for sustained use of grasslands. Because elk were virtually sole users of grasslands in winter, the potential for intraspecific competition may have been considerable.

Concentration areas were used almost exclusively by the species indicated for each area example. Therefore, considering management guidelines for individual cervid species and their preferred habitats may be a practical strategy for maintaining adequate populations and forage on the BCWMA.

Several management considerations evolved during the course of this study. Causes for concern that would require immediate reduction of elk, MD or WTD densities were not observed. However, several long-term strategies should be considered that would improve forage conditions and winter habitat effectiveness for each cervid species.

First, the 1,000-1,500 sustainable elk population target is excessive (BCWMA Draft Rev. Manage. Plan, MDFWP, Missoula, 1989). Evidence of substantial forage use, frequent dispersal of subgroups from the main herd to areas adjacent the study area, and dispersal of the main herd after the 1991 wildfire indicated that forage resources and possibly space were becoming increasingly limited on the study area. Observed dispersal of elk from normally preferred foraging areas may have been a demonstration of adaptive behavior that minimized passive intraspecific competition on the study area (Geist 1982). I believe the potential of the BCWMA to maintain 1,000-1,500 elk for an indefinite period of time is low for the aforementioned reasons; however, 1,000-1,200 elk could possibly be supported for shorter periods of 1-3 years. Results from this study also supported the continued heavy harvest of resident elk and deer because of their greater apparent destructive influence on forage species during spring and summer (this study, Young and Payne 1948).

Second, although the 1991 wildfire burned approximately 33% of the study area; serviceberry mainstems aged during this study indicated that much of the remaining area had not burned for at least 25-30 years. Historic mean fire intervals for the majority of habitats on the study area were between 10-30 years (Losensky 1987). Advanced forest succession, resulting from recent fire exclusion, was expected to continually reduce productivity of understory herbaceous forage and shrubs. Although tall deciduous shrubs did not appear to be highly preferred by elk, MD or WTD during this study, levels of observed use indicated that they were an important integral component of cervid diets in winter. Further, successional advances in the absence of fire were expected to continually reduce productivity of shrubs regardless of utilization intensity by cervids (Hemmer 1975).

Much of the vegetation that occurs on the BCWMA is fire-adapted and could respond well to an appropriate fire treatment (Noste and Bushey 1987). Winter habitat improvement as a result of burning would benefit elk, MD and WTD (Makela 1990). Therefore, strong consideration should be given to reintroducing fire to these plant communities.

Third, DelSordo (1993), Hurley (1994) and results from this study have indicated that areas with dense-mature overstory canopy are limited in abundance on the BCWMA. Habitats with dense-mature overstory canopies can mitigate influences of severe winter weather for elk and MD, and are of special importance for WTD (this study, Moen 1968, Beall 1974, Moen 1976, Geist 1981, Walmo and Schoen 1981, Skovlin

1982). Therefore, future timber management planning on the BCWMA should include the deferral of additional forested habitats to be managed as dense-mature forest for severe winter cover. This strategy would be especially important for WTD winter range located along Highway 83. Appropriate sizes for such habitat units should be further investigated.

Fourth, I would recommend the re-evaluation of the management objective of maximum sustainable utilization of the winter range by elk, MD and WTD (BCWMA Draft Rev. Manage. Plan, MDFWP, Missoula, 1989). Skepticism has been expressed by various authors regarding the plausibility of management for high stable wildlife populations (Wallmo et al. 1977, Potvin and Huot 1983, Botkin 1990, Mackie et al. 1990). This skepticism is based upon the premise that constancy in nature rarely if ever exists (Botkin 1990). This is likely true for cervid/winter-forage relationships on the BCWMA.

An alternative would be to manage elk and deer populations at fluctuating levels over time. Habitat manipulations for winter forage maintenance (such as prescribed burning) are periodically necessary as a result of normal forest succession (Hemmer 1975). Habitat treatments could be accomplished during periods with low cervid populations, which would allow treated vegetation to respond in the absence of intensive use. Elk and deer reductions could be accomplished through increased harvest.

Initially, reduced elk and deer use would facilitate post-burn plant responses and improve potential long-term productivity. However, substantial use of browse 2-4 years after treatment may then be desirable for maintaining shrubs within reach (Aldous 1952, Krefting et al. 1966), and for enhancing their productivity (Shepherd 1971). Productive winter habitats would allow for periodic increases of elk and deer numbers above normal management target levels. Some long-term benefits would include increased forage quality for cervids, forage productivity, plant community integrity, and economic benefits. Monitoring should also be included in all phases of such a strategy.

LITERATURE CITED

Aldous, S. E. 1952. Deer browse clipping study in the Lake States region. J. Wildl. Manage. 16:401-409.

Anderson, A. F., D. E. Medin, and D. C. Bowden. 1972. Mule deer numbers and shrub yield utilization on winter range. J. Wildl. Manage. 36:571-578.

Anthony, R. G., and N. S. Smith. 1974. Comparison of rumen and fecal analysis to describe deer diets. J. Wildl. Manage. 38:535-540.

_____, and _____. 1977. Ecological relationships between mule deer and white-tailed deer in southeastern Arizona. Ecol. Monogr. 47:255-277.

Asherin, D. A. 1976. Changes in elk use and available browse production on north Idaho winter ranges following prescribed burning. Pages 122-134 in S. R. Heib, ed. Elk-logging-roads symposium proceedings. Univ. of Idaho, Moscow.

Baker, R. H. 1984. Origin, classification and distribution. Pages 1-18 in L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

Baremore, W. J. 1980. Population characteristics, distribution and habitat relationships of six ungulates in northern Yellowstone Park. Fin. Rep. Yellowstone Files.

Baty, G. R., C. L. Marcum, and M. J. Thompson. 1993. Observations of elk and deer competition and commensalism on a western Montana winter range. Pages 58-62 in J. D. Cada, J. G. Peterson and T. N. Lonner, comps., Proc. Western States and Prov. Elk Workshop, Mont. Dept. of Fish, Wildl. and Parks, Bozeman. 72pp.

Beall, R. C. 1974. Winter habitat selection and use by a western Montana elk herd. Ph.D. Thesis, Univ. Montana, Missoula. 197pp.

Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. Sci. Amer. 225(1):86-93.

Berner, K. L. 1985. Winter and spring habitat selection by white-tailed deer in a western Montana second-growth forest. M.S. Thesis, Univ. Montana, Missoula. 98pp.

Boll, L. A. 1958. Elk nutrition - the response of elk calves to various winter diets under controlled conditions. M.S. Thesis, Montana State Univ., Missoula. 101pp.

Botkin, D. B. 1990. Discordant harmonies. Oxford Univ. Press, New York, N.Y. 241pp.

Bryant, L. D., and C. Maser. 1982. Classification and distribution. Pages 1-59 in J. W. Thomas and D. E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa.

Caughley, G. 1979. What is this thing called carrying capacity? Pages 2-8 in M.S. Boyce and L.D. Hayden-Wing, eds. North American elk: ecology, behavior and management. Univ. Wyoming Press, Laramie.

Cheatum, E. L. 1949. Bone marrow as an index of malnutrition in deer. N.Y. State Conserv. 3:19-22.

Clover, M. R., 1956. A single gate deer trap. Calif. Fish and Game, Sacramento. 42:199-201.

Cole, G. F. 1957a. A browse survey method for use on Montana big game ranges. Mont. P-R Project W-37-R-8. 12pp.

______. 1957b. Browse survey supplement note. Mont. P-R Project W-37-R-9. 5pp.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Connolly, G. E. 1981. Assessing populations. Pages 287-345 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. of Nebraska Press, Lincoln.

Constan, K. J. 1972. Winter foods and range use of three species of ungulates. J. Wildl. Manage. 36:1068-1076.

Crouch, G. L. 1981. Effects of deer on forest vegetation. Pages 449-457 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. of Nebraska Press, Lincoln.

Dahlberg, B. L., and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin, Wis. Conserv. Dept. Tech. Wildl. Bull. 14.

Davitt, B. B., and J. R. Nelson. 1980. A method of preparing plant epidermal tissues for use in fecal analysis. College of Agriculture Research Center Circular. 0628, Washington State Univ., Pullman, Wa. 3pp.

Dearden, B. L., R. E. Pegau, and R. M. Hansen. 1975. Precision of microhistological estimates of ruminant food habitats. J. Wildl. Manage. 39:402-407.

DelSordo, D. 1993. Mapping the understory of forested elk habitat using remote sensing and geographic information systems. M.S. Thesis, Univ. Montana, Missoula. 61pp.

Denniston, R. H. 1956. Ecology, behavior, and population dynamics of the Wyoming or Rocky Mountain moose, Alces alces shirasi. Zoologica 41:105-118.

Dietz, D. R., R. H. Udall, and L. E. Yeager. 1962. Chemical composition and digestibiltiy by mule deer of selected forage species, Cache la Poudre Range, Colorado. Colo. Game and Fish Dept. Tech. Publ. No. 14. 89pp.

Dimock, E. J., R. R. Silen, and V. E. Allen. 1976. Genetic resistance in Douglas-fir to damage by snowshoe hare and black-tailed deer. For. Sci. 22:106-121.

Dunbar, R. I. M. 1978. Competition and niche separation in a high altitude herbivore community in Ethiopia. E. Afr. Wildl. J. 16:183-199.

Fuller. P. R. 1976. Browse production and utilization on the Spotted Bear Mountain winter range and seasonal movements of the Spotted Bear elk herd. M. S. Thesis, Univ. Montana., Missoula. 66pp.

Geis, A. F. 1954. The food requirements and relative digestibility of a variety of winter diets fed to elk (Cervus canadensis nelsoni) under controlled conditions. M.S. Thesis, Montana State Univ., Missoula. 68pp.

Geist, V. 1981. Behavior: adaptive strategies in mule deer. Pages 157-223 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. of Nebraska Press, Lincoln.

______. 1982. Adaptive behavioral strategies. Pages 219-

277 in J. W. Thomas and D. E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa.

Gill, G. B. 1972. Alterations of the in vitro digestibility of deer browse as affected by systematic mixing of paired species. M.S. Thesis, Univ. Montana, Missoula. 82pp.

Gill, R. B., L. H. Carpenter, R. M. Bartmann, D. L. Baker, and G. G. Schoonveld. 1983. Fecal analysis to estimate mule deer diets. J. Wildl. Manage. 47:902-915.

Greer, K. R., and H. W. Yeager. 1967. Sex and age indications from upper canine teeth of elk (wapiti). J. Wildl. Manage. 32:408-417.

______, J. B. Kirsch, and H. W. Yeagher. 1970. Seasonal food habits of the northern Yellowstone elk (wapiti) herds during 1957 and 1962-1967 as determined from 793 rumen samples. Fed. Aid Final Rep. Proj. W-83-R-12, J-B-1. Helena: Montana Dep. Fish and Game. 76pp.

Hamlin, K. L., and R. J. Mackie. 1989. Mule deer in the Missouri River Breaks, Montana: a study of population dynamics in a fluctuating environment. Fed. Aid in Wildl. Restor., Job Compl. Rept., Proj. W-120-R, Mont. Dept. Fish, Wildl. and Parks, Helena. 401pp.

Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. J. Range Manage. 35:146-151.

______, and K. A. Hanley. 1982. Food resource partitioning by sympatric ungulates on Great Basin rangeland. J. Range Manage. 35:152-158.

Hansen, R. M., and L. D. Reid. 1975. Diet overlap of deer, elk and cattle in southern Colorado. J. Range Manage. 28:43-47.

______, and R. C. Clark. 1977. Foods of elk and other ungulates at low elevations in northwestern Colorado. J. Wildl. Manage. 41:76-80.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292-1297.

Hartkorn, F., and M. Rognrud. 1956. Deer surveys. MT Fish and Game Comm., Wildl. Rest. Div., Wildl. Inv.-District 2, Job Comp. Rep. No. W-72-R-1-A-1, Missoula. 22pp.

Helwig, L. L. 1957. The value of conifers as a winter feed for elk (Cervus canadensis nelsoni) determined under controlled conditions. M.S. Thesis, Montana State Univ., Missoula. 79pp.

Hemmer, D. M. 1975. Serviceberry: ecology, distribution, and relationships to big game. M.S. Thesis, Univ. Montana, Missoula. 76pp.

Hicks, L. L. 1990. Habitat use by white-tailed deer in relation to winter range silviculture treatments in the Thompson River drainage, northwestern Montana. Ph.D. Thesis, Univ. Montana, Missoula. 79pp.

Hirst, S. M. 1975. Ungulate-habitat relationships in a South African woodland/savanna ecosystem. Wildl. Monogr. 44. 60pp.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. of Washington Press, Seattle. 730pp.

Hobbs, N. T., D. L. Baker, and R. B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. J. Wildl. Manage. 47:1-16.

Holechek, J. L., M. Vavra, and R. D. Pieper. 1982a. Botanical composition determination of range herbivore diets: a review. J. Range Manage. 35:309-315.

_____, _____, S. Mady Dabo, and T. Stephenson. 1982b. Effects of sample preparation, growth stage, and observer on microhistological analysis. J. Wildl. Manage. 46:502-505.

_____, and R. Valdez. 1985. Magnification and shrub stemmy material influences on fecal analysis accuracy. J. Range Manage. 38:350-352.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419-424.

Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. Macmillan Publ. Co. Inc., New York, N.Y. 474pp.

Hudson, R. J., D. M. Hebert, and V. C. Brink. 1976. Occupational pattern of wildlife on a major east Kootenay winter-spring range. J. Range Manage. 29:38-43.

Hurley, M. A. 1994. Summer-fall ecology of the Blackfoot-

Clearwater elk herd of western Montana. M.S. Thesis, Univ. Idaho, Moscow. 138pp.

Janke, D. M. 1977. White-tailed deer population characteristics, movements, and winter site selection in western Montana. M.S. Thesis, Univ. Montana, Missoula. 92pp.

Jarman, P. J., and A. R. E. Sinclair. 1979. Feeding strategy and the pattern of resource partitioning in ungulates. Pages 130-163 in A. R. E. Sinclair and M. Norton-Griffiths, eds. Serengeti-dynamics of an ecosystem. Univ. of Chicago Press, Chicago, Ill.

Jenkins, K. J. 1985. Winter habitat and niche relationships of sympatric cervids along the North Fork of the Flathead River, Montana. Ph.D. Thesis, Univ. Idaho, Moscow. 183pp.

______, and R. G. Wright. 1987. Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. Can. J. of Zool. 65:1397-1401.

______, and ______. 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. J. Appl. Ecol. 25:11-24.

Jensen, C. H., and G. W. Scotter. 1977. A comparison of twig-length and browsed-twig methods of determining browse utilization. J. Range Manage. 30:64-67.

Johnson, R. R. 1980. Elementary statistics. Third ed. Duxbury Press. North Scituate, Mass. 607pp.

Julander, O. 1958. Techniques in studying competition between big game and livestock. J. Range Manage. 11:18-21.

Knight, R. R. 1970. The Sun River elk herd. Wildl. Monogr. 23. 66pp.

Knoche, K. G. 1968. The ecology of the Rattlesnake Creek, Montana mule deer range. M.S. Thesis, Univ. Montana, Missoula. 152pp.

Kramer, A. 1973. Interspecific behavior and dispersion of two sympatric deer species. J. Wildl. Manage. 37:288-300.

Krefting, L. W., M. H. Stenlund, and R. K. Seemel. 1966. Effects of simulated and natural deer browsing on mountain maple. J. Wildl. Manage. 30:481-488.

Kufeld, R. C. 1973. Foods eaten by the Rocky Mountain elk. J. Range Manage. 26:106-113.

_____, O. C. Wallmo, and C. Feddema. 1973. Foods of the Rocky Mountain mule deer. USDA Forest Service Research Paper. RM-111. 31pp.

Lack, D. 1945. The ecology of closely related species with special reference to cormorant (Phalacrocorax carbo) and shag (P. aristotelis). J. Anim. Ecol. 14:12-16.

Leuthold, W. 1978. Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. Oecologia 35:241-252.

Lewis, S. W. 1994. Fecal and rumen analyses in relation to temporal variation in black-tailed deer diets. J. Wildl. Manage. 58:53-58.

Lonner, T. N. 1972. Age distributions and some relationships of key browse plants on big game ranges in Montana. M. S. Thesis. Montana State Univ., Bozeman. 79pp.

Losensky, B. J. 1987. A strategy to implement ecosystem maintenance burning on the Lolo National Forest. U.S. For. Serv., Lolo Nat. For., Missoula, Montana. Unpubl. Rep. 89pp.

Lyon, L. J. 1970. Length- and weight-diameter relations of serviceberry twigs. J. Wildl. Manage. 34:456-460.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.

Mackie, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River breaks, Montana. Wildl. Monogr. 20. 79pp.

_____. 1976. Interspecific competition between mule deer, other game animals, and livestock. Pages 49-54 in J. B. Low ed. Mule deer decline in the West: a symposium. Utah State Univ. Agric. Exp. Sta., Logan. 134pp.

_____, K. L. Hamlin, D. F. Pac, G. L. Dusek, and A. K. Wood. 1990. Compensation in free-ranging deer populations. Trans. 55th N.A. Wildl. and Nat. Res. Conf., Denver, Colo. pp 518-526.

Macnab, J. 1983. Wildlife management as scientific experimentation. Wildl. Soc. Bull. 11:397-401.

Makela, P. D. 1990. Effects of prescribed burning on the Burdette Creek winter range. M.S. Thesis, Univ. Montana, Missoula. 112pp.

Marcum, C. L. 1975. Summer-fall habitat selection and use by a western Montana elk herd. Ph.D. Thesis, Univ. Montana, Missoula. 188pp.

_____, and D. O. Loftsgaarden. 1980. A nonmapping technique for studying habitat preferences. J. Wildl. Manage. 44:963-968.

May, R. M. 1975. Some notes on estimating the competition matrix, a. Ecology 56:737-741.

McCullough, M. E. 1955. Balance of ration nutrients and efficiency of feed utilization by ruminants. J. Range Manage. 8:61-65.

Miller, R. S. 1967. Pattern and process in competition. Adv. Ecol. Res. 4:1-74.

Moen, A. N. 1968. Energy exchange of white-tailed deer, western Minnesota. Ecology 49:676-682.

_____. 1976. Energy conservation by white-tailed deer in winter. Ecology 57:192-198.

_____. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. J. Wildl. Manage. 42:715-738.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ., Ser. E. Biol. 3:65-80.

Morris, M. S., and J. E. Schwartz. 1957. Mule deer and elk food habitats on the National Bison Range. J. Wildl. Manage. 21:189-193.

Nagy, J. G., H. W. Steinhoff, and G. M. Ward. 1964. Effects of essential oils of sagebrush on deer rumen microbial function. J. Wildl. Manage. 28:785-790.

_____, T. Hakonson, and K. L. Knox. 1969. Effects of quality of food intake in deer. Trans. 34th N. Am. Wildl. and Nat. Res. Conf. 5pp.

Nelson, J. R. 1982. Relationships of elk and other large herbivores. Pages 415-441 in J. W. Thomas and D. E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa.

_____. 1984. A modeling approach to large herbivore competition. Pages 491-524. in Developing Strategies for Rangeland Management. National Research Council/National Academy of Sciences Publication. Westview press, Boulder, Co. 2,022 pp.

_____, and T. A. Leege. 1982. Nutritional requirements and food habits. Pages 323-369 in J. W. Thomas and D. E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa.

Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildl. Monogr. 77. 53pp.

Norusis, M. J. 1988. The SPSS guide to data analysis for SPSSx. SPSS Inc., Chicago, Ill. 402pp.

Noste, N. V., and C. L. Bushey. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. U.S. For. Serv. Gen. Tech. Rep. INT-239. 22pp.

Pac, D. F., R. J. Mackie, and H. E. Jorgensen. 1991. Mule deer population organization, behavior, and dynamics in a northern Rocky Mountain environment. Fed. Aid in Wildl. Restor., Job Compl. Rept., Proj. W-120-R. Montana Dept. of Fish, Wildl. and Parks, Helena. 316pp.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474-488.

Peek, J. M. 1984. Northern Rocky Mountains. Pages 497-504 in L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

_____, L. W. Krefting, and J. C. Tappeiner. 1971. Variation in twig diameter-weight relationships in northern Minnesota. J. Wildl. Manage. 35:501-507.

Pengelly, W. L. 1954. Idaho Fish and Game Department Job Completion Report. Fed. Aid Proj. W-90-R.

Picton, H. D., and R. R. Knight. 1970. A numerical index of winter conditions of use in big game management. Pages 29-38 in A. O. Haugen ed. Proc. Symp. on snow and ice in relation to wildlife and recreation. Iowa State Univ., Ames, Ia.

Pitt, M. D., and F. E. Schwab. 1990. Assessment of a nondestructive method for estimating browse use. J. Wildl. Manage. 54:175-179.

Potvin, F., and J. Huot. 1983. Estimating carrying capacity of a white-tailed deer wintering area in Quebec. J. Wildl. Manage. 47:463-475.

Radwan, M. A. 1972. Differences between Douglas-fir genotypes in relation to browsing preference by black-tailed deer. Can. J. For. Res. 2:250-255.

Ricklefs, R. E. 1979. Ecology. 2nd ed. Chiron Press, Publ., New York, N.Y. 966pp.

Ryan, K. C., and N. V. Noste. 1985. Evaluating prescribed fires. Pages 230-238 in J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch, tech. coords. Proc. Symposium and workshop on wilderness fire. U.S. For. Serv. Gen. Tech. Rep. INT-182.

Salter, R. E. and R. J. Hudson. 1980. Range relationships of feral horses with wild ungulates and cattle in western Alberta. J. Range Manage. 33:266-271.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carlson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. J. Wildl. Manage. 51:622-630.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

______. 1982. The controversy over interspecific competition. Am. Sci. 70:586-595.

______. 1983. Field experiments on interspecific competition. Am. Nat. 122:240-285.

Schwab, F. E., M. D. Pitt, and S. W. Schwab. 1987. Browse burial related to snow depth and canopy cover in northcentral British Columbia. J. Wildl. Manage. 51:337-342.

Schwartz, C. C., and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. J. Appl. Ecol. 18:343-353.

Scott, M. D. 1978. Elk habitat selection and use on an undisturbed summer range in western Montana. M.S. Thesis, Univ. Montana, Missoula. 98pp.

Seeley, C. R. 1985. Effects of timber harvesting on deer winter ranges and deer use near Missoula, Montana. M.S. Thesis, Washington State Univ., Pullman. 74pp.

Severinghaus, C. A. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Manage. 13:195-216.

Shafer, E. L. 1963. The twig-count method for measuring hardwood deer browse. J. Wildl. Manage. 27:428-437.

Shepherd, H. R. 1971. Effects of clipping key browse species in southwestern Colorado. Tech. Pub. no. 28. Denver: Colorado Division of Game, Fish and Parks. 104pp.

Sinclair, A. R. E. 1977. The African buffalo: a study of resource limitation of populations. Univ. Chicago Press, Chicago, Ill. 355pp.

Singer, F. J. 1979. Habitat partitioning and wildfire relationships of cervids in Glacier National Park, Montana. J. Wildl. Manage. 43:437-444.

Skovlin, J. M. 1982. Habitat requirements and evaluations. Pages 369-413 in J. W. Thomas and D. E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa.

Slott, B. J. 1980. White-tailed deer movements, survival, and population characteristics in the Clearwater River drainage, Montana. M.S. Thesis, Univ. Montana, Missoula. 62pp.

Smith, A. D. 1959. Adequacy of some important browse species in overwintering of mule deer. J. Range Manage. 12:8-13.

Smith, J. G. and O. Julander. 1953. Deer and sheep competition in Utah. J. Wildl. Manage. 17:101-112.

Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscope technique. J. Range Manage. 21:264-265.

Stansberry, B. J. 1991. Ecology of mule deer in coniferous forest habitat in western/northwestern Montana. M.S. Thesis, Montana State Univ., Bozeman. 64pp.

Steele, R. W. 1978. Weather data summary 1956-1978, Lubrecht Experimental Forest, Greenough, Montana. Mont. For. and Cons. Exp. Sta. Misc. Pap. 11. School of For., Univ. Montana, Missoula. 36pp.

______. 1981. Weather data summary 1957-1980, Lubrecht Experimental Forest, Greenough, Montana. Mont. For. and

Cons. Exp. Sta. Misc. Pap. 13. School of For., Univ. Montana, Missoula. 28pp.

Stickney, P. F. 1966. Browse utilization based on percentage of twig numbers browsed. J. Wildl. Manage. 30:204-206.

Taber, R. D., K. Raedeke, and D. A. McCaughran. 1982. Population characteristics. Pages 279-298 in J. W. Thomas and D. E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa.

Telfer, E. S. 1970. Winter habitat selection by moose and white-tailed deer. J. Wildl. Manage. 34:553-559.

_____. 1978. Cervid distribution, browse and snow cover in Alberta. J. Wildl. Manage. 42:352-361.

_____, and J. P. Kelsall. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Can. J. of Zool. 57:2153-2159.

_____, and _____. 1984. Adaptation of some large North American mammals for survival in snow. Ecology 65:1828-1834.

Thompson, M. J., R. E. Henderson, T. O. Lemke, and B. A. Sterling. 1989. Evaluation of a collapsible clover trap for elk. Wildl. Soc. Bull. 17:287-290.

Unsworth, J. W., F. A. Leban, G. A. Sargeant, E. O. Garton, M. A. Hurley, and J. R. Pope. 1991. Aerial Survey: User's Manual. Idaho Dept. Fish and Game, Boise. 54pp.

Vavra, M., R. W. Rice, and R. M. Hansen. 1978. A comparison of esophageal fistula and fecal material to determine steer diets. J. Range Manage. 31:11-13.

Verme, L. J. 1968. An index of winter weather severity for northern deer. J. Wildl. Manage. 32:566-574.

_____, and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91-118 in L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

Wallmo, O. C. 1981. Mule and black-tailed deer distribution and habitats. Pages 1-25 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. of Nebraska Press, Lincoln.

_____, L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. J. Range Manage. 30:122-127.

_____, and W. L. Regelin. 1981. Rocky Mountain and intermountain habitats. Part 1. Food habits and nutrition. Pages 387-398 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. of Nebraska Press, Lincoln.

_____, and J. W. Schoen. 1981. Coniferous forest habitats. Part 2. Forest management for deer. Pages 434-448 in O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. of Nebraska Press, Lincoln.

White, G. C., and R. A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. J. Wildl. Manage. 50:509-513.

Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48:1285-1301.

Wiens, J. A., and J. T. Rotenberry. 1979. Diet niche relationships among North American grassland and shrubsteppe birds. Oecologia 42:253-292.

Wood, A. K., R. J. Mackie, and K. L. Hamlin. 1989. Ecology of sympatric populations of mule deer and white-tailed deer in a prairie environment. Mont. Dep. Fish, Wildl. and Parks, Helena. 97pp.

Wydeven, A. P. and R. B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. J. Wildl. Manage. 49:805-813.

Young, V. A., and G. F. Payne. 1948. Utilization of "key" browse species in relation to proper grazing practices in cutover western white pine lands in northern Idaho. J. For. 46:35-40.

APPENDIX A

Understory cover taxa and substrates observed on the BCWMA mid-summer 1992. Number of plot occurrance (Freq), frequency within stand types (Stnd typs), %composition weighted by stand type area sampled (%Comp), and %frequency within 1,873 plots (%Freq) are given. Nomenclature follows Hitchcock and Cronquist (1973).

Taxon/Substrate	Common Name	Code	Freq	Stnd typs	%Comp	%Freq
Acer glabrum	Rocky Mountain Maple	ACGL	127	11	0.678	6.781
Achillea millefolium	Common Yarrow	ACMI	903	20	0.572	48.211
Agropyron spicatum	Bluebunch Wheatgrass	AGSP	380	14	0.834	20.288
Agropyron spp.	Other Wheatgrass	AGRO	22	7	0.050	1.175
Agrostis scabra	Bentgrass	AGRS	25	7	0.018	1.335
Agrostis stolonifera	Red Top	AGST	59	12	0.197	3.150
Allium spp.	Wild Onion	ALLI	43	13	0.011	2.296
Alnus sinuata	Sitka Alder	ALSI	30	6	0.261	1.602
Amelanchier alnifolia	Serviceberry	AMAL	727	19	3.262	38.815
Anaphalis margaritaceae	Pearly Everlasting	ANMA	31	9	0.012	1.655
Anemone patens	Pasque Flower	ANPA	1	1	0.000	0.053
Antennaria microphylla	Pussytoes	LOMA	229	16	0.236	12.226
Antennaria spp.	Other Pussy-toes	ANTE	288	20	0.160	15.376
Apiaceae Family	Wild Parsley/Hemlock	CIDO	33	4	0.040	1.762
Apocynum androsaemifolium	Dogbane	APAN	67	11	0.162	3.577
Arctostaphylos uva-ursi	Bearberry	ARUV	103	14	0.113	5.499
Arnica spp.	Arnica	ARNI	574	17	0.676	30.646
Artemisia cana	Silver Sage	ARCA	26	6	0.043	1.388
Artemisia frigida	Fringed Sage	ARFR	12	4	0.015	0.641
Artemisia tripartita	Three-Tipped Sage	ARTP	6	1	0.004	0.320
Aster conspicuus	Aster	ASCO	568	15	1.798	30.326
Asteraceae family	Other Asters	ASTE	363	18	0.281	19.381
Astragalus spp.	Vetches	ASTR	182	19	0.108	9.717
Balsamorhiza sagittata	Arrowleaf Balsamroot	BASA	298	15	1.119	15.910
Bare Soil	Bare Soil	BARS	1171	20	18.818	62.520
Berberis repens	Oregon Grape	BERE	968	19	2.340	51.682
Betula occidentalis	Water Birch	BEOC	9	4	0.073	0.481
Brassicaceae Family	Mustards	BRAS	294	17	0.241	15.697
Bromus inermis	Smooth Brome	BRIN	25	9	0.049	1.335
Bromus japonicus	Japanese Brome	JABR	8	2	0.012	0.427
Bromus marginatus	Mountain Brome	BROM	359	18	0.229	19.167
Bromus tectorum	Cheatgrass	BRTE	113	11	0.207	6.033
Calamagrostis rubescens	Pine Grass	CARU	1085	18	3.766	57.928
Campanula spp.	Harebell	CAMP	4	3	0.001	0.214
Capsella bursa-pastoris	Shepherd's Purse	CABU	1	1	0.001	0.053
Carex filifolia	Threadleaf Sedge	CAFI	168	5	0.594	8.970
Carex geyeri	Elk Sedge	CAGE	1101	20	2.696	58.783
Carex spp.	Other Upland Sedges	CARE	316	17	0.172	16.871
Castilleja spp.	Indian Paintbrush	CAST	17	7	0.006	0.908
Ceanothus velutinus	Shiny-Leaf Ceanothus	CEVE	60	3	0.100	3.203
Centaurea maculosa	Spotted Knapweed	CEMA	465	19	1.948	24.826
Chimaphila umbellata	Prince's Pine	CHUM	81	10	0.036	4.325
Cirsium spp.	Musk and Canada Thistles	CIRS	162	17	0.361	8.649

Taxon/Substrate	Common Name	Code	Freq	Stnd typs	%Comp	%Freq
Clematis hirsutissima	Virgin's Bower	CLHI	68	12	0.032	3.631
Clematis occidentalis	Virgin's Bower	CLOC	168	14	0.149	8.970
Clintonia uniflora	Queen Cup Bead-Lily	CLUN	9	2	0.002	0.481
Collinsia parviflora	Blue-Eyed Mary	COPA	18	4	0.008	0.961
Cornus canadensis	Bunchberry Dogwood	COCA	4	1	0.008	0.214
Cornus stolonifera	Redozier Dogwood	COST	48	6	0.282	2.563
Cretaegus douglasii	Hawthorn	CRDO	16	5	0.105	0.854
Cryptantha affinis	Miner's Candle	SPAN	13	1	0.019	0.694
Cyperaceae Family	Mesic Rushes and Sedges	CYPE	6	4	0.023	0.320
Danthonia californica	California Oatgrass	DACA	1	1	0.000	0.053
Danthonia intermedia	Intermediate Oatgrass	DAIN	51	12	0.021	2.723
Elymus glaucus	Wild Rye	ELYM	239	14	0.170	12.760
Epilobium angustifolium	Fireweed	EPAN	326	17	0.263	17.405
Equisetum spp.	Horse Tail	EQUI	61	8	0.147	3.257
Euphorbia esula	Leafy Spurge	EUES	5	2	0.024	0.267
Festuca idahoensis	Idaho Fescue	FEID	475	20	0.782	25.360
Festuca occidentalis	Western Fescue	FEOC	1	1	0.002	0.053
Festuca scabrella	Rough Fescue	FESC	433	14	2.791	23.118
Festuca spp.	Fescue-Unidentified	FEST	1	1	0.000	0.053
Filago arvensis	Fluffweed	CELA	54	7	0.050	2.883
Fragaria virginiana	Wild Strawberry	FRVI	891	19	1.253	47.571
Galium boreale	Bedstraw	GABO	222	16	0.149	11.853
Galium triflorum	Bedstraw	GATR	64	10	0.034	3.417
Geranium viscosissimum	Sticky Geranium	GEVI	293	17	0.475	15.643
Geum triflorum	Prairie Smoke	GETR	63	13	0.038	3.364
Grindelia squarrosa	Curly-Cup Gumweed	GRSQ	2	2	0.001	0.107
Heracleum lanatum	Cow Parsnip	HELA	12	2	0.127	0.641
Heuchera spp.	Alumroot	HECY	111	16	0.045	5.926
Hieracium cynoglossoides	Hawkweed	HICY	310	19	0.185	16.551
Hordeum jubatum	Foxtail Barley	HOJU	1	1	0.000	0.053
Hypericum perforatum	St. John's-Wort	HYPE	4	4	0.003	0.214
Iris missouriensis	Wild Iris	IRIS	2	2	0.002	0.107
Koeleria cristata	Prairie Junegrass	KOCR	276	14	0.307	14.736
Liliaceae Family	Lily-Unidentified	LILY	3	1	0.002	0.160
Linaria vulgaris	Butter and Eggs	LIVU	6	4	0.012	0.320
Linnaea borealis	Twinflower	LIBO	280	14	0.411	14.949
Lithospermum ruderale	Stoneseed	LIRU	151	14	0.131	8.062
Litter	Litter	LITT	1868	20	28.523	99.733
Lonicera ciliosa	Climbing Honeysuckle	LOCI	3	1	0.004	0.160
Lonicera utahensis	Utah Honeysuckle	LOUT	127	15	0.131	6.781
Lupinus spp.	Lupines	LUPI	620	17	1.781	33.102
Mentha arvensis	Mint	MEAR	7	1	0.010	0.374
Mentha spicata	Mint	MESP	12	4	0.008	0.641
Menziesia ferruginea	False Huckleberry	MEFE	24	4	0.059	1.281
Mertensia spp.	Blue Bells	MERT	7	1	0.006	0.374
Moss	Moss	MOSS	546	18	0.483	29.151
Orthocarpus tenuifolius	Owl Clover	ORTE	66	7	0.029	3.524
Osmorhiza chilensis	Sweet Cicely	ARNU	33	8	0.010	1.762

Taxon/Substrate	Common Name	Code	Freq	Stnd typs	%Comp	%Freq
Other Forbs	Other Forbs	UNKF	615	20	0.458	32.835
Other Grass	Other Grass	UNKG	40	11	0.019	2.136
Pachistima myrsinites	Mountain Lover	PAMY	140	10	0.053	7.475
Penstemon spp.	Beardtongue	PENS	196	17	0.072	10.464
Phacelia heterophylla	Phacelia	MUEA	56	7	0.105	2.990
Philadelphus lewisii	Mock Orange	PHLE	7	1	0.015	0.374
Phleum pratense	Timothy	PHPR	272	19	0.279	14.522
Physocarpus malvaceus	Ninebark	PHMA	2	1	0.005	0.107
Poa spp.	Bluegrass	POAS	296	20	0.901	15.804
Polypodiaceae Family	Ferns	FERN	14	5	0.003	0.747
Potentilla fruiticosa	Shrubby Cinquefoil	POFR	5	1	0.010	0.267
Potentilla spp.	Cinquefoil	POTE	270	18	0.392	14.415
Prunus virginiana	Chokecherry	PRVI	52	8	0.105	2.776
Pyrola spp.	Pyrola	PYRO	21	8	0.005	1.121
Rhamnus alnifolia	Buckthorn	RHAL	13	5	0.052	0.694
Rhamnus cathartica	Buckthorn	RHCA	2	1	0.002	0.107
Ribes spp.	Current/Gooseberry	RIBE	63	11	0.122	3.364
Rock	Rocks (>10cm Diameter)	ROCK	477	19	1.009	25.467
Rosa woodsii	Woods Rose	ROWO	512	20	0.629	27.336
Rubus idaeus	Wild Raspberry	RUID	12	5	0.035	0.641
Rubus parviflorus	Thimbleberry	RUPA	97	16	0.169	5.179
Salix bebbiana	Beb Willow	SALI	10	4	0.016	0.534
Salix scouleriana	Upland Willow	SASC	59	13	0.163	3.150
Sambucus spp.	Elderberry	SAMB	1	1	0.000	0.053
Scirpus microcarpus	Bulrush	SCIR	14	6	0.154	0.747
Senecio triangularis	Arrow-Leaf Groundsel	SETR	22	4	0.015	1.175
Shepherdia canadensis	Buffaloberry	SHCA	41	11	0.091	2.189
Smilacina racemosa/S. stellata	False Solomon's Seal	SMIL	280	15	0.219	14.949
Solidago missouriensis	Goldenrod	SOMI	60	14	0.107	3.203
Sorbus scopulina	Mountain Ash	SOSC	3	2	0.003	0.160
Spiraea betulifolia	Spiraea	SPBE	936	18	3.718	49.973
Stipa columbiana	Columbia Needlegrass	STIP	76	10	0.173	4.058
Stipa richardsonii	Richardson's Needlegrass	STRI	95	10	0.238	5.072
Streptopus amplexifolius	Twisted Stalk	STAM	171	15	0.114	9.130
Symphoricarpos albus	Snowberry	SYAL	968	18	5.245	51.682
Taraxacum spp.	Dandelion	TAOF	130	18	0.061	6.941
Thalictrum occidentale	Western Meadow Rue	THOC	590	17	0.693	31.500
Thlaspi arvense	Penny Cress	THAR	4	3	0.003	0.214
Trifolium spp.	Clover/Alfalfa	TRIF	76	16	0.090	4.058
Typha latifolia	Cattail	TYLA	3	1	0.001	0.160
Urtica dioica	Stinging Nettle	URDI	9	3	0.006	0.481
Vaccinium caespitosum	Dwarf Huckleberry	VACA	11	5	0.015	0.587
Vaccinium globulare	Blue Huckleberry	VAGL	234	15	0.432	12.493
Vaccinium scoparium	Grouse Whortleberry	VASC	4	1	0.003	0.214
Veratrum californicum	False Hellebore	VECA	1	1	0.000	0.053
Verbascum thapsus	Wooly Mullein	VETH	82	11	0.042	4.378
Viola spp.	Violet	VIOL	194	18	0.061	10.358
Wood	Wood (>10cm Diameter)	WOOD	795	18	2.433	42.445
Xerophyllum tenax	Beargrass	XETE	54	7	0.069	2.883

APPENDIX B

Methods for Mobility Resistance (MR), Snow Severity (SS) and Winter Severity (WS) Indices

A drop-penetrometer (DP) was constructed for estimating snow crust/density properties that were expected to limit winter movements of elk, mule deer and white-tailed deer. The DP was constructed from a pine dowel measuring 1-m long x 3.25-cm diameter. The lower end was drilled and weighted with 85 g of lead for added stability during measurements. The dowel was marked in centimeters and coated with 3 heavy coats of polyurethane sealer to minimize variations in dowel weight during wet weather. The lower end was slightly rounded instead of pointed to increase the DP's sensitivity to snow resistance variables.

Each week from 1 January-28 February, five readings were taken at each site and averaged to mitigate the potential bias of occasional erratic measurements. The DP was dropped from a constant 1 m above the snow surface and the distance traveled below the snow surface was recorded in cm. The DP was then manually forced the remaining distance to the ground surface and the snow depth was recorded. The sinking depth of the DP was used as a measure of cervid mobility resistance due to snow crust, density and depth. A similar method was described by Verme (1968). Sinking depth was expressed as

$$\bar{x}_{pi}/\bar{x}_{di} \times 100 = S_i$$

Appendix B (continued)

where $\bar{x}_{pi}$ = mean distance DP traveled below snow surface at survey site i, $\bar{x}_{di}$ = mean snow depth at survey site i, and S_i = % sinking depth at site i.

Weekly $\bar{x}_p$'s and $\bar{x}_d$'s for each site were combined and averaged for the months of January and February (1992 and 1993) and a winter S_i was calculated. This was done in order to derive a cumulative winter estimate for each site.

The assumption was made that the greatest % sinking depth (100%) implied the least measurable mobility resistance. Observations of mobility resistance in the field at the time of survey generally supported this assumption. In order to express mobility resistance from low to high a mobility resistance index was derived

$$100-S_i = MR_i$$

where MR_i = index of % mobility resistance at site i scaled with low to high values. Because a derived S_i is also presumably a function of depth, these indices weight depth somewhat higher than crust and density variables. It was assumed that the influence of % mobility resistance and snow depth were relatively equal in their influence on cervid behavior and when combined would provide an estimate of the total cost of snow to wintering cervids on a given site. Two sites in 1993 had MR's of 0 which would have incorrectly estimated the influences of snow as 0. Therefore all MR's

Appendix B (continued)

<0.5% were assigned a default value of 0.5% in order to acknowledge the presence of snow. The index combining all snow variables was expressed as

$$(MR_i x D_i)/100 = SS_i$$

where D_i = Mean winter snow depth (cm) at site i, and SS_i = Snow severity index for combined snow resistance variables (ie. mobility resistance and depth) at site i. The SS has a minimum (min) value of (0.5% x 1)/100 = .005 and continuous maximum (max) value of (100% x max depth) /100 = max SS.

Methods for the Winter Severity Indices (MR,D and T)

Weekly max and min temperatures (°C) were recorded for 5 sites during January and February 1992 and 1993. Mean monthly max and min temperatures were calculated for both years for each site. Monthly averages were combined to derive a winter average max and min for each site. The winter max and min values for each site were then combined into one temperature value as

$$-(\bar{x}_{mi} + \bar{x}_{ni})/2 = T_i$$

where $\bar{x}_{mi}$ = the mean combined January-February (winter) max temperature at site i, $\bar{x}_{ni}$ = the mean combined January-February (winter) min temperature at site i, and T_i = winter temperature value for site i, which provides a proportional temperature rank for each site. An equalizing coefficient was derived in order to weight temperature equally with snow

Appendix B (continued)

conditions

$$-SS_m/T_n = EQ$$

where SS_m = the greatest SS for both years, T_n = the lowest winter temperature value for both years (must be < 0° C), and EQ = temperature equalizing coefficient.

eg. 26.3 = SS_m

-9.75 = T_n

EQ = -26.3/-9.75 = 2.7

All T_i values were multiplied by the EQ which yielded a temperature index

$$T_i \times EQ = T_{ri}$$

where T_{ri} = the equalized temperature index for site i. The T_{ri} was added to the SS_i following Verme (1968) for the index sum. In order to scale the lowest index value at 1, -1.425 was added to all index sums. This yielded the winter severity index

$$T_{ri} + SS_i - 1.425 = WS_i$$

where WS_i = winter severity index for site i.

APPENDIX C

Mean percentages of forage species in winter diets from fecal analysis of elk, mule deer and white-tailed deer on the Blackfoot-Clearwater Wildlife Management Area, 1992. Winter diets (Win) are for January, February and March combined.

Forage Taxon	Elk Jan	Elk Feb	Elk Mar	Elk Win	Mule Deer Jan	Mule Deer Feb	Mule Deer Mar	Mule Deer Win	White-Tailed Deer Jan	White-Tailed Deer Feb	White-Tailed Deer Mar	White-Tailed Deer Win
Forbs												
Achillea millefolium	0	0	0	0	0	0	0	1	0	0	1	0
Antennaria spp.[1]	0	0	0	0	0	0	T	T	0	0	2	1
Aster spp.	0	0	0	0	0	0	0	0	0	0	1	0
Astragalus spp.[1]	0	0	0	0	0	0	T	T	0	0	0	0
Balsamorhiza sagittata	T	1	T	T	0	2	2	2	1	4	3	3
Castilleja spp.	0	0	0	0	0	0	0	0	0	0	1	0
Centaurea maculosa	0	0	0	0	T	0	0	T	0	0	0	0
Cirsium spp.	0	0	0	0	0	0	0	0	0	0	1	0
Equisetum spp.[1]	0	1	0	0	0	0	0	0	0	0	0	0
Fragaria virginiana	0	0	0	0	0	0	1	0	0	0	T	0
Galium spp.	0	0	0	0	0	0	0	0	0	0	1	T
Lupinus spp.[1]	0	2	T	1	0	T	0	0	1	2	2	2
Mertensia spp.[1]	0	0	0	0	0	1	T	0	0	0	0	1
Mustard	0	0	0	T	0	0	0	0	0	0	T	T
Trifolium spp.[1]/Alfalfa	0	0	0	0	T	0	0	0	0	0	0	0
Verbascum thapsus	0	0	0	0	0	0	0	0	0	T	0	0
Other Forbs	1	T	T	T	0	1	2	2	3	6	2	1
Subtotal	1	4	1	1	T	4	5	5	5	12	14	8
Graminoids												
Agropyron spicatum	3	10	4	4	1	0	2	1	0	0	1	2
Agropyron spp.[1]	0	0	0	0	0	1	0	0	0	0	0	0
Agrostis spp.	0	0	1	0	0	0	0	0	0	0	0	0
Bromus spp.	3	1	0	1	0	0	1	1	T	1	2	2
Calamagrostis rubescens	1	3	T	0	0	0	0	0	0	T	0	0
Dactylis glomerata	0	0	0	0	0	1	0	0	0	0	1	T

Appendix C (continued)

Forage Taxon	Elk Jan	Elk Feb	Elk Mar	Elk Win	Mule Deer Jan	Mule Deer Feb	Mule Deer Mar	Mule Deer Win	White-Tailed Deer Jan	White-Tailed Deer Feb	White-Tailed Deer Mar	White-Tailed Deer Win
Graminoids												
Elymus glaucus	1	0	0	0	0	1	0	0	0	0	0	0
Festuca spp.	0	0	0	0	0	0	0	0	0	2	0	0
Festuca idahoensis	1	3	4	3	1	1	4	3	3	2	3	2
Festuca scabrella	9	18	28	20	1	0	3	1	4	0	6	5
Koeleria cristata	2	2	2	T	0	0	1	0	0	1	T	1
Phleum pratense	1	0	0	0	0	0	1	1	0	0	0	0
Poa spp.	2	5	4	4	T	3	1	1	2	2	5	4
Stipa spp.[1]	2	9	7	5	0	1	4	2	1	2	1	T
Grass[1]	1	1	0	0	0	0	0	0	0	0	2	0
Carex spp.[1]	34	16	28	25	0	7	3	8	1	8	T	3
Subtotal	60	68	78	62	3	15	20	18	11	18	21	19
Deciduous Shrubs												
Acer glabrum	0	0	0	0	1	T	0	T	0	0	0	0
Amelanchier alnifolia	7	12	1	8	7	7	0	3	12	2	0	6
Betula occidentalis	T	0	0	3	2	0	0	0	0	0	0	0
Cretaegus douglasii	0	0	0	0	0	0	1	0	0	0	0	0
Lonicera spp.	0	0	0	0	0	T	0	0	0	0	0	0
Menziesia ferruginea	0	0	0	0	2	0	0	0	0	0	0	T
Philadelphus lewisii	0	0	0	0	0	T	0	0	0	0	0	0
Populus spp.[1]	0	0	0	0	T	0	1	0	0	0	0	0
Prunus virginiana	0	0	0	0	1	0	0	0	0	0	0	0
Rosa woodsii	0	0	0	0	2	0	0	0	0	0	0	0
Rubus parviflorus	0	1	0	0	0	0	1	1	1	0	0	0
Salix spp.	7	1	4	7	3	1	0	2	6	T	2	3
Sambucus spp.[1]	0	0	0	0	0	0	2	1	0	1	0	0
Shepherdia canadensis	0	0	0	T	0	0	0	0	1	0	0	1

Appendix C (continued)

Forage Taxon	Elk				Mule Deer				White-Tailed Deer			
	Jan	Feb	Mar	Win	Jan	Feb	Mar	Win	Jan	Feb	Mar	Win
Deciduous Shrubs												
Symphoricarpos albus	1	0	0	0	0	0	0	T	0	0	0	0
Shrubs[1]	0	0	0	0	T	1	0	T	0	0	2	T
Subtotal	15	14	5	18	18	9	5	7	20	3	4	10
Evergreen Shrubs												
Arctostaphylos uva-ursi	0	0	0	0	1	0	0	0	0	0	0	0
Artemisia spp.[1]	0	T	0	0	0	T	0	0	0	0	0	1
Berberis repens	1	3	7	7	3	21	25	18	2	14	28	11
Ceanothus velutinus	0	0	0	0	2	1	0	1	0	0	0	0
Chrysothamnus spp.[1]	0	0	0	0	0	0	0	0	0	1	1	0
Linnaea borealis	0	0	0	0	0	0	0	0	0	0	1	0
Ribes spp./Berberis[2]	1	0	8	4	0	7	9	9	1	4	8	5
Subtotal	2	3	15	11	6	29	34	28	3	19	38	17
Conifers												
Abies lasiocarpa	0	0	0	0	1	0	0	0	1	0	0	0
Juniperus scopulorum	2	1	0	0	0	1	2	0	0	0	0	T
Larix occidentalis	0	0	0	0	1	1	0	0	0	0	0	0
Pinus spp.[1]	3	5	0	5	9	6	3	3	15	13	3	7
Pseudotsuga menziesii	11	3	0	3	55	31	30	38	40	31	19	35
Conifer Bark	6	2	1	0	6	4	1	1	5	4	0	4
Subtotal	22	11	1	8	72	43	36	42	61	48	22	46
Other												
Lichen[3]	0	0	0	0	1	T	T	T	0	0	1	0
Seed/Nut	T	0	0	0	0	0	0	0	T	0	0	T
Composite Family	0	0	0	0	0	0	0	0	0	0	T	0
Subtotal	0	0	0	0	1	0	0	T	0	0	1	T

Appendix C (continued)

[1]Species were not distinguished.

[2]Ribes spp. and Berberis repens were occasionally indistinguishable in the feces.

[3]Lichen was under represented due to destruction during analysis.

APPENDIX D

Mean percentages of forage species in winter diets from fecal analysis of elk, mule deer and white-tailed deer on the Blackfoot-Clearwater Wildlife Management Area, 1993. Winter diets (Win) are for January, February and March combined.

	Elk				Mule Deer				White-Tailed Deer			
Forage Taxon	Jan	Feb	Mar	Win	Jan	Feb	Mar	Win	Jan	Feb	Mar	Win
Forbs												
Achillea millefolium	0	0	0	0	0	0	0	0	0	0	T	1
Anaphalis margaritacea	0	0	0	1	0	0	0	0	0	0	0	0
Antennaria spp.[1]	0	0	0	0	0	0	0	0	0	0	0	T
Arnica spp.[1]	T	0	0	0	T	0	T	1	0	0	2	1
Aster spp.[1]	0	0	0	0	0	0	0	0	0	0	T	0
Balsamorhiza sagittata	1	0	T	1	1	3	1	2	1	1	4	4
Castilleja spp.[1]	0	0	0	0	0	0	0	0	0	0	1	1
Centaurea maculosa	0	0	0	0	0	0	0	0	1	1	0	0
Fragaria virginiana	0	0	0	0	0	0	T	0	0	0	0	0
Galium spp.[1]	0	0	0	0	0	0	T	0	0	0	T	0
Lupinus spp.[1]	0	T	1	1	1	0	0	T	0	0	1	1
Mertensia spp.[1]	0	0	0	0	0	0	1	1	0	0	0	T
Mustard	0	0	1	0	0	0	T	1	0	0	T	0
Trifolium spp.[1]/Alfalfa	T	0	0	0	0	0	0	0	0	0	0	0
Verbascum thapsus	0	0	0	0	T	0	1	1	0	0	0	T
Other Forbs	1	T	1	1	1	T	2	2	1	0	2	1
Subtotal	2	T	3	4	3	3	5	8	3	2	10	9
Graminoids												
Agropyron spicatum	0	0	0	2	0	0	0	0	0	0	0	0
Agropyron spp.[1]	2	4	4	0	0	2	1	0	0	1	2	1
Agrostis spp.[1]	1	3	T	0	0	2	0	0	0	1	1	T
Bromus spp.[1]	1	2	2	1	0	0	0	0	0	0	1	1
Calamagrostis rubescens	1	1	2	1	0	0	0	0	0	0	0	0
Dactylis glomerata	0	0	2	1	0	0	0	0	0	0	0	0
Elymus glaucus	1	1	1	0	0	0	0	0	0	0	0	0

Appendix D (continued)

Forage Taxon	Elk Jan	Elk Feb	Elk Mar	Elk Win	Mule Deer Jan	Mule Deer Feb	Mule Deer Mar	Mule Deer Win	White-Tailed Deer Jan	White-Tailed Deer Feb	White-Tailed Deer Mar	White-Tailed Deer Win
Graminoids												
Festuca idahoensis	3	7	3	2	0	0	3	0	0	2	3	6
Festuca scabrella	41	34	18	40	1	2	1	1	4	1	2	3
Hordeum jubatum	0	0	0	0	0	0	1	0	0	0	1	1
Koeleria cristata	7	4	2	5	0	1	T	0	0	T	0	T
Phleum pratense	1	0	2	2	0	0	0	0	0	0	2	T
Poa spp.	8	5	10	4	0	T	1	1	5	1	7	3
Stipa spp.[1]	13	4	5	5	T	0	0	0	T	1	2	1
Grass[1]	T	2	1	0	0	0	0	0	0	1	0	0
Carex spp.[1]	3	10	16	12	3	3	5	4	3	2	7	4
Subtotal	82	77	68	75	4	10	12	6	12	10	28	20
Deciduous Shrubs												
Acer glabrum	0	T	0	1	2	1	1	1	1	2	0	2
Amelanchier alnifolia	0	4	6	2	8	1	2	2	7	3	T	3
Betula occidentalis	0	0	0	0	0	0	1	0	0	0	0	1
Cornus stolonifera	0	T	0	0	T	1	1	T	T	0	0	T
Cretaegus douglasii	0	0	1	0	0	0	0	0	0	1	0	0
Physocarpus malvaceus	0	0	0	0	0	1	T	1	T	0	0	0
Populus spp.	0	0	1	0	0	0	0	0	0	0	0	0
Prunus virginiana	0	1	0	T	0	0	0	T	0	0	0	0
Rosa woodsii	0	0	2	2	0	0	0	0	0	0	0	2
Rubus parviflorus	T	0	0	0	0	0	0	0	0	0	0	0
Salix spp.	4	3	2	2	4	4	4	3	3	2	2	2
Shepherdia canadensis	0	T	0	0	2	1	0	0	3	0	T	T
Symphoricarpos albus	0	0	0	0	0	0	0	0	0	0	0	1
Shrubs[1]	T	0	0	T	0	3	2	3	1	0	2	1
Subtotal	4	8	12	7	16	12	11	10	15	8	4	12

Appendix D (continued)

Forage Taxon	Elk Jan	Elk Feb	Elk Mar	Elk Win	Mule Deer Jan	Mule Deer Feb	Mule Deer Mar	Mule Deer Win	White-Tailed Deer Jan	White-Tailed Deer Feb	White-Tailed Deer Mar	White-Tailed Deer Win
Evergreen Shrubs												
Arctostaphylos uva-ursi	0	0	0	0	0	0	0	0	0	5	0	6
Artemisia spp.[1]	1	T	0	1	T	0	0	T	0	0	5	1
Berberis repens	T	0	13	1	4	1	8	4	2	T	13	10
Ceanothus velutinus	0	0	0	0	2	0	1	2	0	0	0	0
Chrysothamnus spp.[1]	0	0	0	0	0	0	0	1	0	0	3	1
Ribes spp./*Berberis*[2]	1	0	1	0	2	0	12	1	T	T	16	1
Subtotal	2	T	14	2	8	1	21	8	2	5	37	19
Conifers												
Abies lasiocarpa	0	0	0	0	0	0	1	1	0	0	0	0
Juniperus scopulorum	0	0	0	0	T	0	1	1	1	0	0	0
Pinus spp.[1]	5	6	T	4	9	13	6	11	22	34	6	23
Pseudotsuga menziesii	5	9	3	8	59	58	41	48	44	38	13	17
Conifer Bark	0	0	0	0	1	3	1	6	1	1	1	T
Subtotal	10	15	3	12	69	74	50	67	68	73	20	40
Other												
Lichen[3]	0	0	0	0	0	0	1	1	0	2	0	0
Moss	0	0	0	0	0	0	0	0	0	0	1	T
Subtotal	0	0	0	0	0	0	1	1	0	2	1	T

[1]Species were not distinguished.

[2]*Ribes* spp. and *Berberis repens* were occasionally indistinguishable in the feces.

[3]Lichen was under represented due to destruction during analysis.

APPENDIX E

Locations of snow measurement sites monitored during the winters of 1992 and 1993 on the BCWMA.

Snow measurement site[a]	Universal Transverse Mercator Coordinates	
	Northing	Easting
Low elevations		
sl-1	52 10 76	03 25 54
sl-2 A	52 11 03	03 22 55
sl-3	52 10 64	03 21 74
sl-4 B	52 13 40	03 19 00
sl-5	52 13 04	03 21 66
Moderate elevations		
sm-1 C	52 11 54	03 25 06
sm-2	52 14 16	03 20 20
sm-3 D	52 13 60	03 23 22
sm-4	52 15 84	03 23 80
sm-5	52 14 60	03 23 90
High elevations		
sh-1	52 12 40	03 24 14
sh-2	52 14 82	03 19 90
sh-3 F	52 15 54	03 21 06
sh-4	52 16 34	03 23 10
sh-5	52 15 16	03 22 55
Northerly aspects		
sn-1	52 15 67	03 19 96
sn-2	52 17 32	03 21 40
sn-3 E	52 16 87	03 22 98
sn-4	52 17 56	03 24 12
sn-5	52 17 46	03 23 27

a = Upper case letters indicate that mean temperatures, snow severity and winter severity indices were calculated for these sites.

APPENDIX F

Squared Weight on Diameter Relationships for Browse Utilization Estimation

Lyon (1970), noted a curvi-linear relationship for the weight-on-diameter relationship of serviceberry twigs. Scatter plots for twigs collected on the BCWMA suggested such a curvi-linear relationship for serviceberry as well as 5 other shrub species of interest, even though regression correlation coefficients were relatively high (average R^2 = 0.83, range = 0.72-0.91). Curvi-linear relationships caused the consistent underestimation of weight for twigs with large and small diameters. This is of concern if such regression equations are used for browse utilization weight estimates. Further, browsed diameter means for plots with high browsed twig numbers (> 50%), occasionally produced negative plot weight estimates when entered into standard weight-on-diameter equations. This was caused by an exaggerated negative Y intercept that resulted when a straight line was fitted to a curvi-linear relationship. Therefore, it was necessary to find functions that more closely fit weight-on-diameter distributions.

Regression equations using the square root of twig weight on twig diameter were constructed. These equations produced consistently greater correlation coefficients for chokecherry, red-osier dogwood, Rocky Mountain maple,

Appendix F (continued)

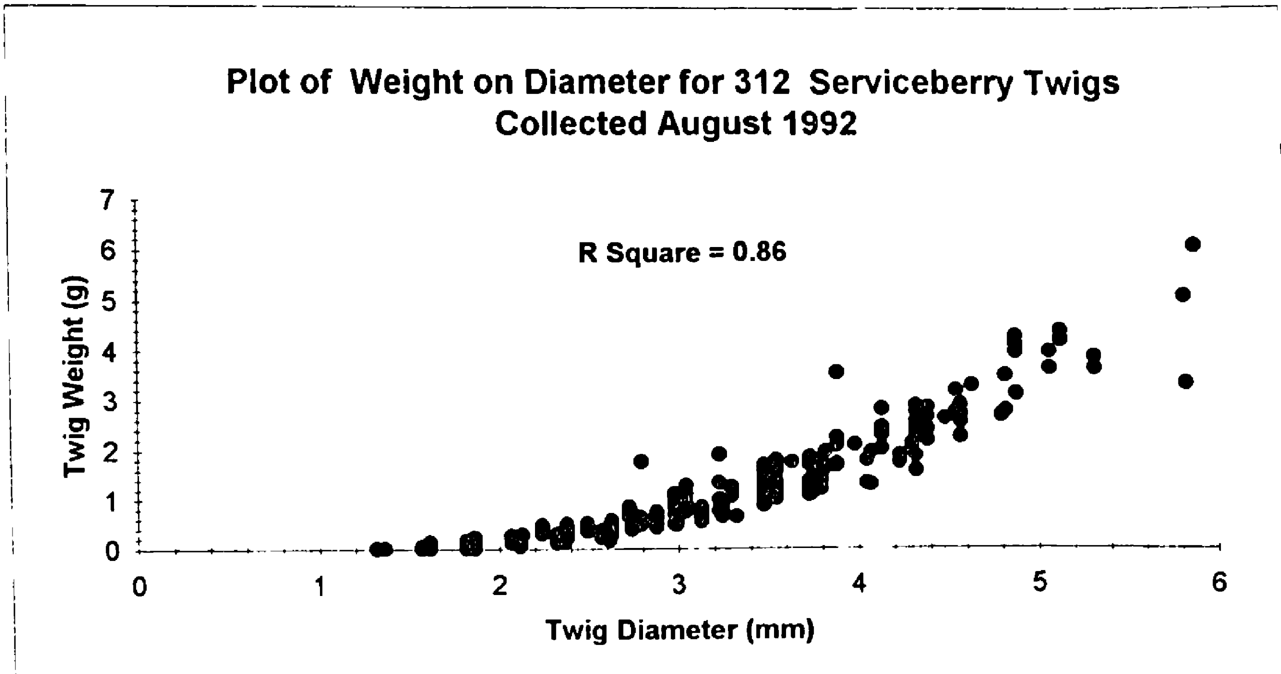
serviceberry, snowbrush ceanothus, and upland willow (average R^2 = 0.92, range = 0.84-0.95). The square root equations prevented negative weight estimates and provided more realistic weight approximations.

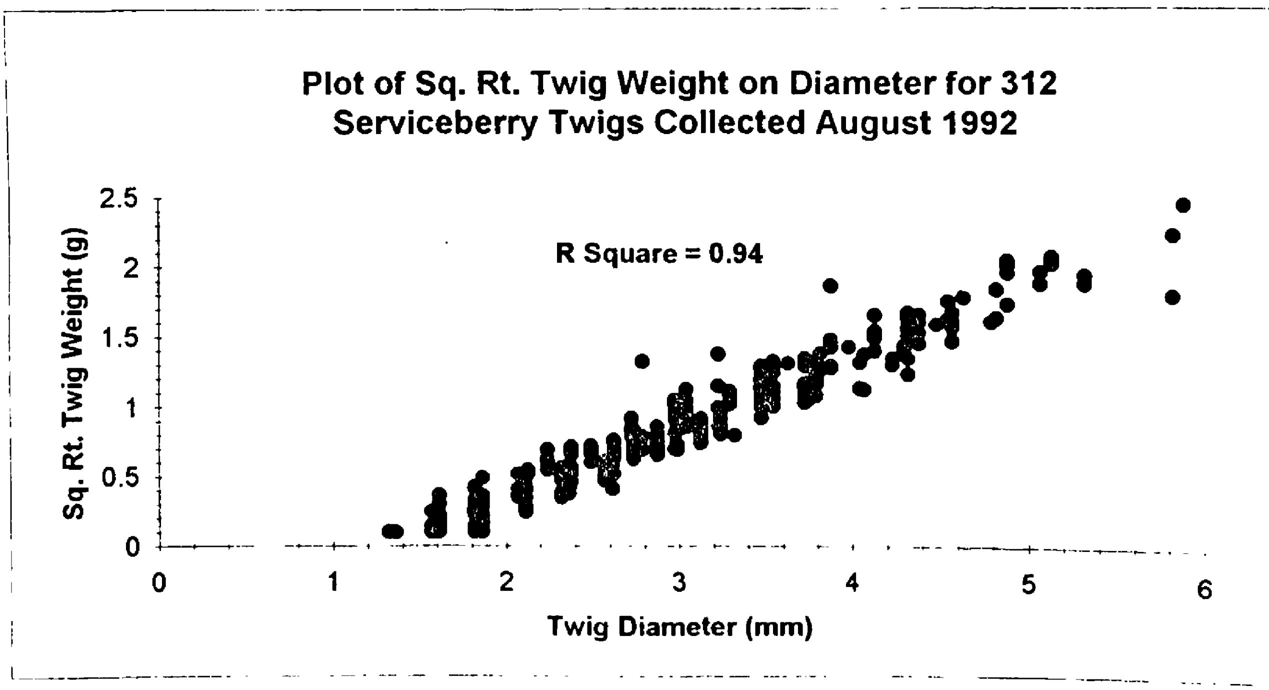
Since the relationship of weight-on-diameter appears to be a square function, the arithmetic mean calculated for diameters is a poor estimator for weight. The weights of large diameter twigs are underestimated in a sample (since weight is proportional to volume), especially when the samples are highly variable. A better estimator used to calculate mean twig diameters for the purpose of weight estimation is:

$$\bar{x}_d = \sqrt{\frac{\Sigma(x_i^2)}{n}}$$

where $\bar{x}_d$ = mean diameter of twigs on a plot, x_i = diameter of sample twig i, and n = number of browsed twigs on a plot. In this manner the mean is taken in the weight rather than the diameter domain.

Appendix F (continued)





APPENDIX G

INFLUENCE OF CATTLE ON SERVICEBERRY PRODUCTIVITY

Introduction

Managers of the Blackfoot-Clearwater Wildlife Management Area wanted information on summer-fall cattle grazing effects on browse productivity to help direct future cattle grazing. Therefore, adjacent grazed and ungrazed sites were selected where current annual growth (CAG) production could be compared.

Sites for this study were located across a fence-line running between the NE 1/4 of the NE 1/4 of Section 33; and the NW 1/4 of the NW 1/4 of Section 34 (T15N, R13W). Section 33 was purchased by the Montana Department of Fish, Wildlife and Parks (MDFWP) from the Dreyer family on 15 November 1989. Roughly 300 AUMs ranged over about 730 ha during the 20-30 years preceding the purchase by MDFWP (M. J. Thompson, MDFWP, pers. commun.). Section 33 was rested from cattle grazing for 2 years prior to this study.

Section 34 was a grazed portion of a ranch owned by the Montana Forest and Conservation Experiment Station, which was previously known as the Bandy Ranch. Cattle grazing intensity on the Bandy Ranch for about 30 years prior to this study was approximately 400 AUMs over about 600 ha (M. J. Thompson, MDFWP, pers. commun.). Sections 33 and 34 were partially forested.

Appendix G (continued)

Methods

On 21 July 1992, an area was selected that had similar vegetation, slope and aspect on both sides of the fence-line between Sections 33 and 34. One random starting point was selected for each side of the fence. From these points 15 serviceberry shrubs (30 total) were selected using the nearest neighbor method (Cole 1957b). All shrubs selected were mature plants > 3 years of age. All CAG twigs were counted on each shrub, and were tallied in 2 length classes (short = 2.0-14.9 cm, and medium 15.0-26.9 cm). All CAG was clipped from at least 2 mainstems of each shrub. Mainstems represented growth in the 4 cardinal quadrants. Twig samples were sorted by treatment, oven-dried at 100° C for 24 hours (Lyon 1970) and weighed to the nearest 0.01 g. Mean twig weights were calculated for each length class by treatment (grazed or ungrazed). Twig totals for each length class by treatment were multiplied by the corresponding mean twig weights (g) for weight-per-shrub estimates. Student's *t*-test was used to test for differences in mean twig number per shrub and mean weight-per-shrub across treatments. Descriptive data for heights, summer utilization and growth form (Cole 1957a) were recorded for all shrubs sampled.

Results

Browse production, condition and summer utilization results for 15 serviceberry shrubs on the NE 1/4 of the NE 1/4 Section 33 of the MDFWP Dreyer property (ungrazed), and 15 serviceberry shrubs on the NW 1/4 of the NW 1/4 Section 34 (T15N, R13W) of the Bandy Ranch (grazed).

	Dreyer Ranch (ungrazed)	Bandy Ranch (grazed)
Mean short twig weight g ($\pm$95% CI)	0.049(0.011)	0.055(0.011)
Mean medium twig weight g ($\pm$95% CI)	0.313(0.050)	0.357(0.060)
Mean no.twigs/shrub (and SD)[a]	74.6(75.2)	93.9(97.3)
Mean CAG weight g/shrub (and SD)[b]	4.5(5.1)	7.1(6.8)
Shrubs sampled < 0.3 m tall	6	10
Shrubs sampled 0.3-2.0 m tall	9	5
Number of shrubs sampled in 4 leader-use classes[c]		
(0-1%)	0	2
(1-10%)	4	6
(10-40%)	10	6
(40-60%)	1	1
Number of shrubs sampled in 2 growth-form classes[c]		
"Normal"	10	11
"Mutilated"	5	4

a = Mean twig number/shrub not significantly different between treatments (P = 0.549).

b = Mean CAG weight g/shrub not significantly different between treatments (P = 0.248).

c = Leader-use and growth form classes defined by Cole (1957a).

Appendix G (continued)

Discussion

The number of twigs per shrub and weight of CAG (g) per shrub were not significantly different between the grazed and ungrazed sites. This indicated that shrubs rested from cattle grazing had not substantially increased CAG production. On the ungrazed pasture I observed evidence of spring and summer browsing by elk and deer, which may have suppressed shrub productivity (Young and Payne 1948).

It was extremely difficult to locate sites in Sections 33 and 34 where characteristics on both sides of the fence were similar, and production may have been influenced more by past silvicultural treatments than cattle grazing. Also, the treatments may not have been very distinct because of similarities in historic use by cattle. The area sampled did not normally receive substantial winter use by elk and deer, and results obtained for this area may not be applicable to preferred winter ranges. More intensive study over a broad area is needed to more accurately document cattle-serviceberry relationships.

APPENDIX H

Mean twig weight (Wt g), standard deviation (SD), sample size (n), 95% confidence interval (95% CI), and confidence interval % of mean (% CI), by browse type (Br.type), and twig length class (Lgth cl.), for samples collected within 20 m of browse plots during late summer 1991. Acgl=Rocky Mountain maple, Amal= serviceberry, Ceve=ceanothus, Cost=red-ozier dogwood, Prvi=chokecherry, Sasc= upland willow.

Summer 1991

		Acgl					Amal					Ceve				
Br. type[a]	Lgth cl.[b]	Wt g	SD	n	95%CI	%CI	Wt g	SD	n	95%CI	%CI	Wt g	SD	n	95%CI	%CI
1	1	0.076	0.05	50	0.013	16.8	0.127	0.09	50	0.024	18.8	0.520	0.42	99	0.083	15.9
1	2	0.256	0.10	50	0.028	10.9	0.443	0.20	50	0.054	12.2	1.490	0.66	70	0.155	10.4
1	3	0.607	0.21	34	0.070	11.6	1.109	0.34	50	0.093	8.4	2.250	0.87	26	0.351	15.6
1	4	1.245	0.37	11	0.250	20.1	2.111	0.46	15	0.254	12.0	2.410	1.40	4	2.226	92.4
2	1	0.073	0.06	50	0.016	22.4	0.116	0.07	50	0.020	17.0	N/A				
2	2	0.320	0.11	50	0.029	9.1	0.424	0.21	50	0.059	13.9	N/A				
2	3	0.638	0.19	46	0.056	8.7	1.020	0.35	50	0.097	9.5	N/A				
2	4	1.579	0.81	41	0.249	15.7	3.194	1.87	38	0.594	18.6	N/A				
3	1	0.067	0.05	50	0.013	19.4	0.072	0.05	50	0.014	20.0	N/A				
3	2	0.292	0.09	33	0.032	11.0	0.514	0.20	50	0.054	10.5	N/A				
3	3	0.670	0.16	17	0.081	12.0	1.095	0.39	50	0.108	9.9	N/A				
3	4	1.346	0.29	10	0.208	15.5	2.088	0.67	31	0.237	11.4	N/A				
4	1	0.078	0.06	50	0.016	20.3	0.085	0.05	50	0.015	17.6	N/A				
4	2	0.306	0.10	50	0.027	8.7	0.462	0.21	50	0.057	12.4	N/A				
4	3	0.575	0.15	50	0.042	7.2	1.056	0.43	50	0.119	11.3	N/A				
4	4	1.041	0.20	15	0.112	10.7	2.316	0.89	39	0.278	12.0	N/A				

		*Cost					Prvi					Sasc				
Br. type[a]	Lgth cl.[b]	Wt g	SD	n	95%CI	%CI	Wt g	SD	n	95%CI	%CI	Wt g	SD	n	95%CI	%CI
1	1	N/A					0.171	0.13	99	0.025	14.5	N/A				
1	2	N/A					0.755	0.28	76	0.067	8.8	N/A				
1	3	N/A					1.639	0.56	16	0.300	18.3	N/A				
1	4	N/A					N/A					N/A				
2	1	N/A					N/A					0.049	0.04	50	0.011	22.1
2	2	N/A					N/A					0.192	0.09	47	0.026	13.4
2	3	N/A					N/A					0.536	0.17	41	0.057	10.7
2	4	N/A					N/A					1.754	1.12	39	0.351	20.0
3	1	N/A					N/A					0.056	0.05	50	0.014	25.7
3	2	N/A					N/A					0.302	0.12	31	0.042	13.9
3	3	N/A					N/A					0.577	0.14	17	0.069	12.0
3	4	N/A					N/A					2.215	1.07	15	0.590	26.6
4	1	0.108	0.07	99	0.014	13.0	N/A					0.055	0.05	50	0.013	24.2
4	2	0.368	0.11	41	0.035	9.5	N/A					0.254	0.09	42	0.028	10.8
4	3	0.966	0.30	13	0.179	18.5	N/A					0.591	0.19	28	0.072	12.2
4	4	1.823	0.41	4	0.652	35.8	N/A					1.785	0.65	12	0.410	23.0

*Twig samples combined for browse types 3 and 4.

[a] Browse types:1=sites with >20%slope, southerly exposure. 2=sites with >20% slope, northerly exposure. 3=sites with <20%slope, southerly exposure. 4=sites with <20% slope and northerly exposure.

[b] Twig length classes (cm): 1=(2.0-14.9), 2=(15.0-26.9), 3=(27.0-41.9), 4=(42.0<).

~96% of twig weight means have 95% CI's $<\underline{+}30\%$ of the true mean.

APPENDIX I

Mean twig weight (Wt g), standard deviation (SD), sample size (n), 95% confidence interval (95% CI), and confidence interval % of mean (%CI), by browse type (Br.type), and twig length class (Lgth cl.), for samples collected within 20 m of browse plots during late summer 1992. Acgl=Rocky Mountain maple, Amal= serviceberry, Ceve=ceanothus, Cost=red-ozier dogwood, Prvi=chokecherry, Sasc= upland willow.

Summer 1992

		Acgl					Amal					Ceve				
Br. type[a]	Lgth cl.[b]	Wt g	SD	n	95%CI	%CI	Wt g	SD	n	95%CI	%CI	Wt g	SD	n	95%CI	%CI
1	1	0.100	0.07	50	0.018	18.0	0.117	0.10	50	0.026	22.5	0.570	0.44	50	0.122	21.4
1	2	0.317	0.09	50	0.025	7.8	0.521	0.18	50	0.050	9.5	1.902	0.82	50	0.228	12.0
1	3	0.671	0.20	35	0.066	9.8	1.367	0.59	31	0.206	15.1	2.717	0.98	15	0.539	19.8
1	4	1.490	0.40	3	0.991	66.5	2.294	0.35	7	0.322	14.0	4.183	2.40	3	5.953	N/A
2	1	0.083	0.07	50	0.018	22.0	0.100	0.11	50	0.030	29.7	N/A				
2	2	0.283	0.11	50	0.029	10.4	0.536	0.19	50	0.051	9.6	N/A				
2	3	0.739	0.22	50	0.060	8.1	1.199	0.41	26	0.164	13.6	N/A				
2	4	2.167	1.14	44	0.338	15.6	2.746	0.76	8	0.631	23.0	N/A				
3	1	0.111	0.06	50	0.018	16.0	0.099	0.09	50	0.026	25.8	N/A				
3	2	0.306	0.10	50	0.029	9.3	0.515	0.22	50	0.060	11.6	N/A				
3	3	0.702	0.20	44	0.059	8.3	1.219	0.37	50	0.101	8.3	N/A				
3	4	1.601	0.46	15	0.254	15.9	2.522	0.94	42	0.283	11.2	N/A				
4	1	0.070	0.06	50	0.016	22.2	0.107	0.09	50	0.024	22.5	N/A				
4	2	0.358	0.10	50	0.027	7.4	0.441	0.16	50	0.043	9.8	N/A				
4	3	0.641	0.18	50	0.050	7.9	1.150	0.42	50	0.115	10.0	N/A				
4	4	1.480	0.51	47	0.145	9.8	2.665	1.09	31	0.383	14.4	N/A				

		*Cost					Prvi					Sasc				
Br. type[a]	Lgth cl.[b]	Wt g	SD	n	95%CI	%CI	Wt g	SD	n	95%CI	%CI	Wt g	SD	n	95%CI	%CI
1	1	N/A					0.158	0.12	50	0.034	21.2	0.058	0.04	50	0.012	20.1
1	2	N/A					0.668	0.30	30	0.111	16.6	0.262	0.08	24	0.032	12.3
1	3	N/A					1.445	0.36	2	3.242	N/A	0.709	0.24	21	0.109	15.4
1	4	N/A					N/A					1.503	0.58	4	0.927	61.7
2	1	N/A					N/A					0.079	0.05	50	0.015	18.6
2	2	N/A					N/A					0.279	0.13	33	0.044	15.8
2	3	N/A					N/A					0.792	0.30	15	0.166	20.9
2	4	N/A					N/A					3.510	2.47	4	3.927	N/A
3	1	N/A					N/A					0.059	0.05	50	0.015	24.9
3	2	N/A					N/A					0.235	0.08	50	0.022	9.6
3	3	N/A					N/A					0.612	0.18	50	0.051	8.3
3	4	N/A					N/A					1.738	0.88	50	0.245	14.1
4	1	0.091	0.07	99	0.014	15.2	N/A					0.063	0.05	50	0.014	22.0
4	2	0.382	0.15	81	0.032	8.3	N/A					0.330	0.12	50	0.033	9.9
4	3	0.946	0.31	45	0.090	9.5	N/A					0.664	0.25	50	0.068	10.3
4	4	1.934	0.60	14	0.346	17.9	N/A					3.184	3.25	50	0.901	28.3

*Twig samples combined for browse types 3 and 4.

[a] Browse types: 1=sites with >20%slope, southerly exposure. 2=sites with >20% slope, northerly exposure. 3=sites with <20%slope, southerly exposure. 4=sites with <20% slope and northerly exposure.

[b] Twig length classes (cm): 1=(2.0-14.9), 2=(15.0-26.9), 3=(27.0-41.9), 4=(42.0<).

~96% of twig weight means have 95% CI's <±30% of the true mean.

APPENDIX J

Estimates of number of elk days assuming 6 shrub species of interest as sole forage resource, with equal palatability and to be 100% available on the BCWMA 1991-1993.

Elk eat approximately 4.1 kg/day deciduous browse current annual growth (CAG) (for a 225 kg adult cow) (Geis 1954).

Estimate of browse type area estimated from DelSordo (1993) = 6,496 ha.

1,000 elk x 4.1 = 4,100 kg/day.
500 elk x 4.1 = 2,050 kg/day.
250 elk x 4.1 = 1,025 kg/day.

Total Production 1991 = 8.72 kg/ha (with average precipitation during the growing season).

6,496 ha x 8.72 kg = 56,645.1 total kg estimate produced in year 1991.

Total number of browse forage days for elk assuming 100% CAG utilization (non-sustainable).
1,000 elk: 56,645.1/4,100 kg = 13.8 days.

500 elk: 56,645.1/2,050 kg = 27.6 days.

250 elk: 56,645.1/1,025 kg = 55.3 days.

Total number of browse forage days for elk incorporating 50% proper use value (sustainable).
1,000 elk: (56,645.1 x 0.5)/4,100 kg = 6.9 days.

500 elk: (56,645.1 x 0.5)/2,050 kg = 13.8 days.

250 elk: (56,645.1 x 0.5)/1,025 kg = 27.6 days.

Estimates of number of mule deer (MD) days assuming 6 shrub species of interest as sole forage resource, with equal palatability and 100% availability for the BCWMA 1991-1993.

Mule deer eat approximately 1.3 kg/day deciduous browse current annual growth (CAG) (for a 54 kg adult doe) (Smith 1959).

Estimate of browse type area estimated from DelSordo (1993) = 6,496 ha.

1,000 MD x 1.3 = 1,300 kg/day.
500 MD x 1.3 = 650 kg/day.
250 MD x 1.3 = 325 kg/day.

Total Production 1991 = 8.72 kg/ha (with average precipitation during the growing season).

6,496 ha x 8.72 kg = 56,645.1 total kg estimate produced in year 1991.

Total number of browse forage days for MD assuming 100% CAG utilization (non-sustainable).
1,000 MD: 56,645.1/1,300 kg = 43.6 days.

500 MD: 56,645.1/650 kg = 87.1 days.

250 MD: 56,645.1/325 kg = 174.3 days.

Total number of browse forage days for MD incorporating 50% proper use value (sustainable).
1,000 MD: (56,645.1 x 0.5)/1,300 kg = 21.8 days.

500 MD: (56,645.1 x 0.5)/650 kg = 43.6 days.

250 MD: (56,645.1 x 0.5)/325 kg = 87.1 days.

Estimates of number of white-tailed deer (WTD) days assuming 6 shrub species of interest as the sole forage resource, with equal palatability and 100% availability for the BCWMA 1991-1993.

White-tailed deer eat approximately 1.6 kg/day deciduous browse current annual growth (CAG) (for a 45 kg adult doe) (Dahlberg and Guettinger 1956).

Estimate of browse type area estimated from DelSordo (1993)= 6,496 ha.

1,000 WTD x 1.6 = 1,600 kg/day.
500 WTD x 1.6 = 800 kg/day.
250 WTD x 1.6 = 400 kg/day.

Total Production 1991 = 8.72 kg/ha (with average precipitation during the growing season).

6,496 ha x 8.72 kg = 56,645.1 total kg estimate produced in year 1991.

Total number of browse forage days for WTD assuming 100% CAG utilization (non-sustainable).
1,000 WTD: 56,645.1/1,600 kg = 35.4 days.

500 WTD: 56,645.1/800 kg = 70.8 days.

250 WTD: 56,645.1/400 kg = 141.6 days.

Total number of browse forage days for WTD incorporating 50% proper use value (sustainable).
1,000 WTD: (56,645.1 x 0.5)/1,600 kg = 17.7 days.

500 WTD: (56,645.1 x 0.5)/800 kg = 35.4 days.

250 WTD: (56,645.1 x 0.5)/400 kg = 70.8 days.

APPENDIX K

Visual estimates of percent leaders browsed and mean twig length-winter 1992. Estimates were recorded during track counting runs along transects. Browse type 1 = sites with >20% slope, southerly aspect. Browse type 2 = sites with >20% slope, northerly aspect. Browse type 3 = sites with <20% slope, southerly aspect. browse type 4 = sites <20% slope, northerly aspect.

Estimation Period	from	to		Browse Types 1 Mean	1 SD	2 Mean	2 SD	3 Mean	3 SD	4 Mean	4 SD
Run1	12/31/91	1/17/92	% Leaders Browsed	53.40	24.48	33.93	22.03	47.00	22.64	32.83	21.04
			Twig Length (cm)	10.28	3.63	10.07	4.84	11.38	3.37	11.60	2.96
Run2	1/20/92	2/3/92	% Leaders Browsed	68.12	23.65	48.93	24.35	51.60	19.40	54.33	16.23
			Twig Length (cm)	8.74	3.62	9.25	4.30	10.87	2.79	10.36	2.41
Run3	2/4/92	2/18/92	% Leaders Browsed	72.40	19.74	51.07	21.41	56.20	19.49	50.16	19.43
			Twig Length (cm)	8.84	2.87	9.71	4.16	10.11	2.50	10.20	1.98
Run4	2/19/92	3/4/92	% Leaders Browsed	71.20	17.64	43.93	28.36	52.00	10.00	50.00	17.08
			Twig Length (cm)	8.23	3.00	7.62	5.01	10.31	2.15	10.16	2.41
Run5	3/10/92	3/24/92	% Leaders Browsed	66.00	19.47	49.29	24.56	49.00	13.46	51.61	17.00
			Twig Length (cm)	9.50	2.79	9.25	4.63	11.07	2.18	10.53	2.16

APPENDIX L

Visual estimates of percent leaders browsed and mean twig length-winter 1993. Estimates were recorded during track counting runs along transects. Browse type 1 = sites with >20% slope, southerly aspect. Browse type 2 = sites with >20% slope, northerly aspect. Browse type 3 = sites with <20% slope, southerly aspect. Browse type 4 = sites <20% slope, northerly aspect.

				Browse Types							
				1		2		3		4	
Estimation Period	from	to		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Run1	12/30/92	1/15/93	% Leaders Browsed	26.40	18.68	18.93	18.73	15.20	15.64	9.68	10.56
			Twig Length (cm)	10.92	3.05	12.34	3.17	13.36	2.35	13.40	2.27
run2	1/18/93	2/1/93	% Leaders Browsed	54.00	17.20	32.50	17.51	38.60	18.06	35.48	19.76
			Twig Length (cm)	10.57	2.42	12.97	3.35	13.21	2.67	13.44	2.02
Run3	2/5/93	2/22/93	% Leaders Browsed	67.00	16.33	42.86	20.64	43.20	21.21	46.77	16.76
			Twig Length (cm)	9.40	2.77	12.07	4.48	12.80	3.13	12.99	1.79
Run4	2/23/93	3/9/93	% Leaders Browsed	77.20	10.61	48.21	20.72	60.00	22.13	62.58	13.47
			Twig Length (cm)	7.32	2.63	11.16	4.08	10.41	3.50	11.18	2.03
Run5	3/10/93	3/26/93	% Leaders Browsed	72.80	20.21	49.64	21.70	58.80	18.10	54.52	20.18
			Twig Length (cm)	6.35	2.32	10.98	3.33	10.21	3.33	10.08	2.88

APPENDIX M

Number (and %) of observed CAG twigs browsed by species in 7 above-ground height classes during the winters 1992 and 1993 on the BCWMA.

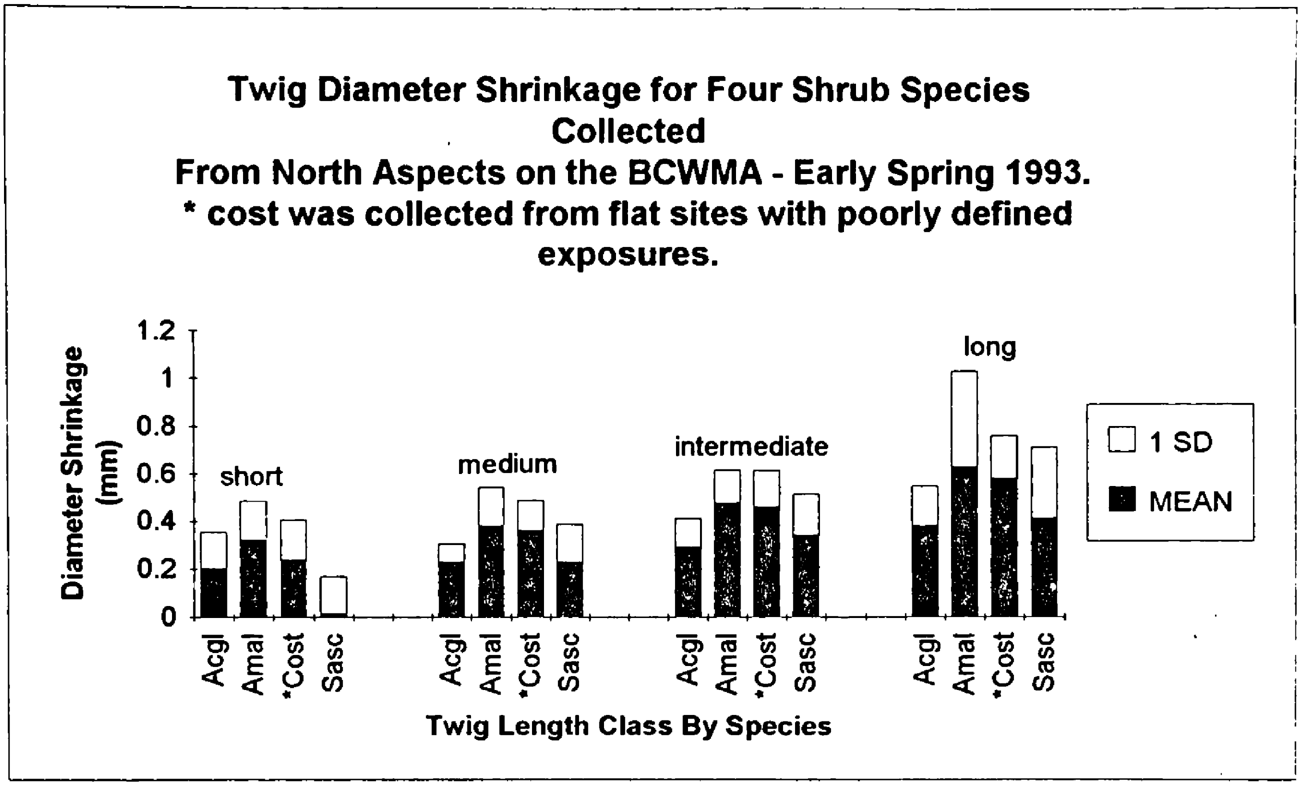
1992

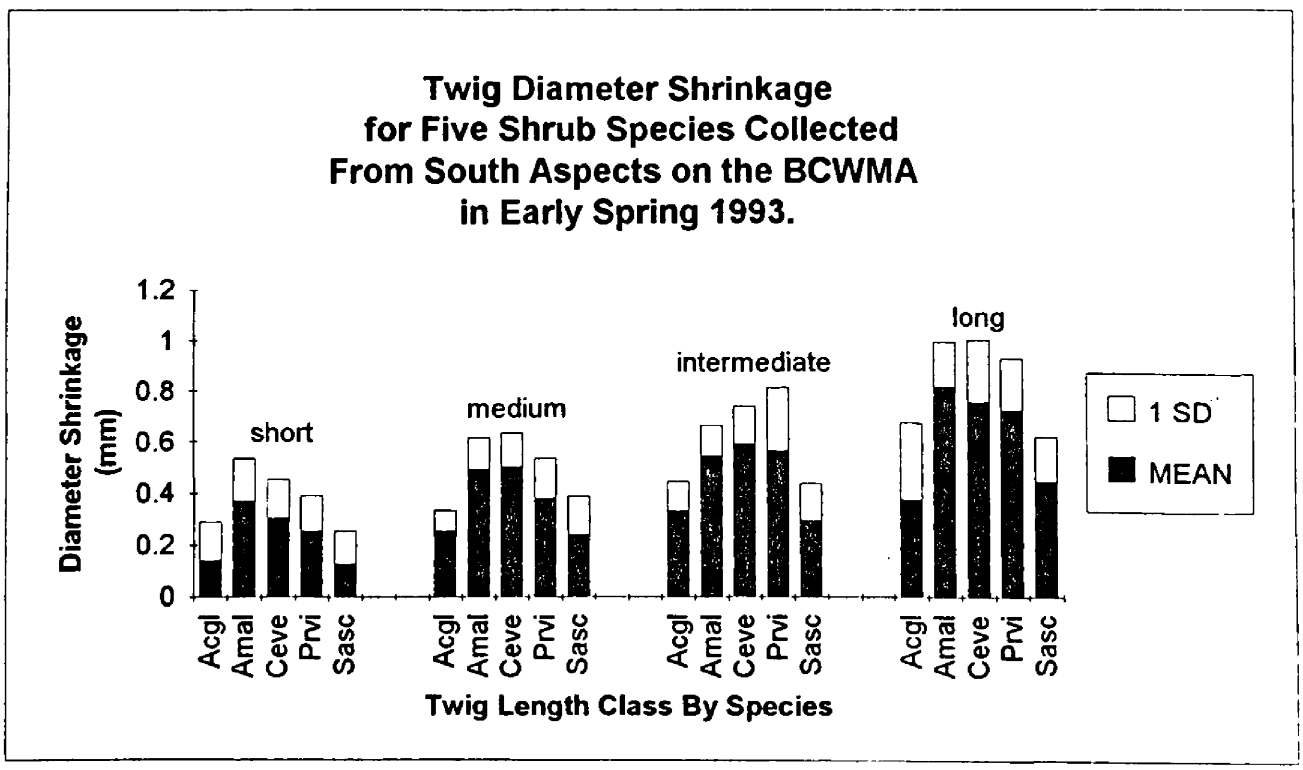
Height Class (cm)	Acgl	Amal	Ceve	Cost	Prvi	Sasc	Sum
0.0-30.5	112(12.6)	586(65.8)	70(7.8)	8(0.9)	89(10.0)	26(2.9)	891(100)
30.6-61.0	69(12.5)	386(69.8)	3(0.5)	19(3.4)	18(3.3)	58(10.5)	553(100)
61.1-91.5	126(16.5)	528(69.2)	0	37(4.8)	9(1.2)	63(8.3)	763(100)
91.6-122.0	75(17.1)	287(65.4)	0	46(10.5)	0	31(7.0)	439(100)
122.1-152.5	9(7.4)	92(76.0)	0	18(14.9)	0	2(1.7)	121(100)
152.6-183.0	20(29.0)	46(66.7)	0	1(1.4)	0	2(2.9)	69(100)
183.0+	3(30.0)	7(70.0)	0	0	0	0	10(100)
Sum (and %)	414(14.5)	1,932(67.9)	73(2.6)	129(4.5)	116(4.1)	182(6.4)	2,846(100)

1993

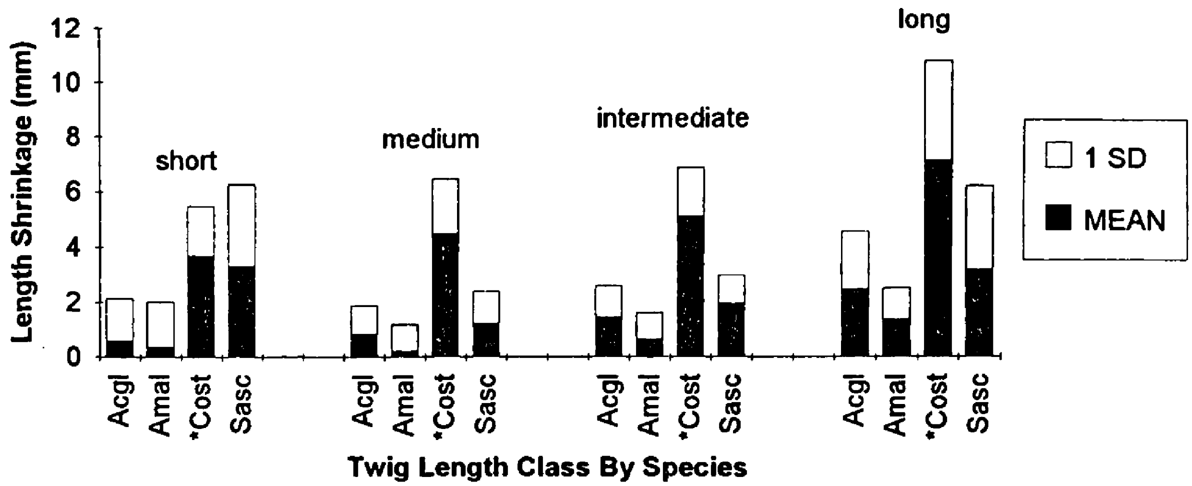
Height Class (cm)	Acgl	Amal	Ceve	Cost	Prvi	Sasc	Sum
0.0-30.5	29(6.7)	234(53.9)	74(17.1)	4(0.9)	80(18.4)	13(3.0)	434(100)
30.6-61.0	46(12.4)	252(68.1)	10(2.7)	6(1.6)	28(7.6)	28(7.6)	370(100)
61.1-91.5	46(8.9)	398(76.8)	7(1.3)	46(8.9)	1(0.2)	20(3.9)	518(100)
91.6-122.0	42(16.9)	185(74.6)	0	10(4.0)	0	11(4.4)	248(100)
122.1-152.5	15(19.8)	52(63.0)	0	12(14.8)	0	2(2.4)	81(100)
152.6-183.0	16(25.4)	34(54.0)	0	10(15.9)	0	3(4.7)	63(100)
183.0+	0	3(42.9)	0	0	0	4(57.1)	7(100)
Sum (and %)	194(11.3)	1,158(67.3)	91(5.3)	88(5.1)	109(6.3)	81(4.7)	1,721(100)

Acgl = Rocky Mountain maple, Amal = Serviceberry, Ceve = Snowbrush ceanothus, Cost = Red-osier dogwood, Prvi = Chokecherry, Sasc = Scouler willow.


Twig Diameter Shrinkage for Four Shrub Species Collected
From North Aspects on the BCWMA - Early Spring 1993.
* cost was collected from flat sites with poorly defined exposures.
Diameter Shrinkage (mm)
1.2
1
0.8
0.6
0.4
0.2
0
short
medium
intermediate
long
Acgl
Amal
*Cost
Sasc
1 SD
MEAN
Twig Length Class By Species


Twig Diameter Shrinkage for Five Shrub Species Collected From South Aspects on the BCWMA in Early Spring 1993.
Diameter Shrinkage (mm)
1.2
1
0.8
0.6
0.4
0.2
0
short
medium
intermediate
long
Acgl
Amal
Ceve
Prvi
Sasc
1 SD
MEAN
Twig Length Class By Species

Twig Length Shrinkage for Four Shrub Species Collected From North Aspects on the BCWMA - Early Spring 1993. *Cost was collected from flat sites with poorly defined exposures.



Twig Length Shrinkage for Five Shrub Species Collected From South Aspects on the BCWMA in Early Spring 1993.